An ecological study of the primates of Southeastern Brazil, with a reappraisal of *Cebus apella* races

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ABSTRACT

SECTION I

The physical characteristics of the Atlantic morphoclimatic domain are described, and its primates are introduced. Emphasis is given to the southeastern part of this domain, in particular to the State of São Paulo, where the intensive study site is.

The study site (Barreiro Rico) is described in detail. Three sub-habitats are identified on the basis of floristic composition and vegetation structure. The phenological behaviour of the forest is delineated. The animal species of medium and large size present at the site are mentioned, as well as their preferences for sub-habitats.

For each of the five primate species of Barreiro Rico, an estimate is given of the population size and structure, and the mechanism of troop spacing is investigated.

Some aspects of the interaction between the primates and their environment are examined, for example, pollination, seed dispersal, seed predation. The diet of each species is examined, and the importance of the phenological cycle in the behaviour of some primate species is discussed. The results are considered from the point of view of conservation.

SECTION II

In this section the sub-specific taxonomy of *Cebus apella* is considered, from an evolutionary point of view.

Several morphological characters (qualitative and quantitative) are examined in skin and skull samples from most of the geographic distribution of *Cebus apella*. The morphological variability within and between localities is assessed. Areas are identified where a number of characters show relative stability. The resulting geographical pattern may be seen as the product of different evolutionary processes. Some of the alternatives are examined. It is suggested that the great morphological variability found in most localities is due to extensive mixture between previously differentiated forms.

The value of the previously described forms is re-examined, but no formal renaming is done.

GENERAL INTRODUCTION

The two sets of Neotropical primates

The Platyrrhini can be divided into two groups: those of the Amazon region and those of the Atlantic coastal region. Such distinction is not arbitrary; these two regions correspond to the two large forested domains (*sensu* Ab'Saber 1977a) which shelter neotropical primates (Fig.1). These two formations were connected in the past, but are now separated by extensive areas of open vegetation and different faunas have evolved in each.

Ten out of the sixteen Platyrrhini genera are endemic to the Amazon region (*Cacajao*, *Chiropotes*, *Pithecia*, *Ateles*, *Lagothrix*, *Cebuella*, *Callimico*, *Saguinus*, *Aotus*, *Saimiri*), but two are endemic to the Atlantic region (*Leontopithecus* and *Brachyteles*). The genera *Alouatta*, *Callithrix* and *Callicebus* are represented by different species in each of the two domains. *Cebus* is also present in both domains, and includes the only platyrrhine species which occupies both domains: *Cebus apella*.

The primate populations of these two regions are not as widely separated as Fig.1 indicates, because some primate species may also occur in the smaller forests of the intervening morphoclimatic domains, e.g. in the gallery forests within the Brazilian "cerrados", in patches of forest within the Venezuelan "llanos" or even in isolated clumps of trees in the "chaco" flooded areas.

Finer distinctions of regional sets could be made. For instance, one might consider the set of primates of the "llanos", or the set from Central America plus the Pacific coast to be different from that of the central Amazon basin. These areas in fact contain

Fig.1 - Distribution of the forested areas in the neotropical realm (dotted areas). Primates are not present in the forested areas at the extreme south of the continent. Most of the Atlantic coastal forest is within Brazilian territory. Copied from Müller 1973 ; drawing originally from Schmithusen,J. (1968) Algemeine Vegetations-geographie, Berlin.

endemic primate species and may have been the site of early evolution for some groups. However, on the grounds that neither of these regions contain endemic genera (which the Atlantic forest does), their primates may be considered part of the broad Amazonian group.

The distinction between these two main primate sets is not only of academic interest; it is also important for practical conservation purposes. The pressures presently faced by these two groups are of different intensities. In the Amazon region, in spite of the alarming rate of deforestation (Fearnside 1982), it is still possible to protect species by preserving large tracts of fairly undisturbed habitat. This is no longer possible in the Atlantic region, where the forest is already too fragmented.

The development of primatology in the Neotropics

Neotropical primates have their distribution restricted to developing countries, where the clash between the necessity of managing the natural resources and the eagerness to exploit them hastily is a well known dilemma. The resulting pressures on primate populations are serious and have been extensively discussed (see Thorington and Heltne 1976, Rainier and Bourne 1977, Chivers and Lane-Petter 1978). The urgency of sensible action has been frequently stated, and so has the dependence of such action on unavailable information of various kinds (e.g. Vanzolini 1967, Thorington and Heltne 1976). Correct management of primate populations depends on information about their distribution, densities, habitat preferences, population dynamics, seasonal stresses, etc., but such information is rarely collected to meet

conservation needs, being rather a function of the researchers' individual fields of interest.

Research effort has been strongly biased towards those species or races inhabiting the northern part of South America, possibly because most research has been done by North-American primatologists. For instance, there is a very extensive literature on Alouatta palliata and Alouatta seniculus (northern part of Alouatta distribution) but almost nothing has been published on Alouatta caraya or Alouatta fusca.

Neotropical primates have been consistently studied since the mid 1960's. Barro Colorado Island (Panama) was the first site where neotropical primates were systematically studied. Carpenter's (1934) pioneer work there was followed by several other medium-term studies (e.g. Hladik and Hladik 1969, Oppenheimer 1968, etc.). Sites in neighbouring countries were soon explored, e.g. in Colombia by Mason (1968), Thorington (1967,1968), in Panama by Baldwin and Baldwin (1972). Sites in Surinam, Peru, Bolivia and particularly in Brazil were not systematically used before the mid 1970's e.g. by Mittermeier (1977), Freese et al. (in prep.), Janson and Terborgh (in prep.), Rylands (1979), Ayres (1981) etc..

Research in Brazilian Amazonia

In 1976 Heltne stated that no information was available on the status of Brazilian populations of Amazonian primates. Since then, a number of surveys and medium-term projects has produced a reasonable amount of information (e.g. Coimbra-Filho and Mittermeier 1977, Branch 1979, Branch in prep., Rylands 1979, Ayres and Milton 1981, Ayres 1981, Ayres and Best 1979, Ayres in press,

etc.).

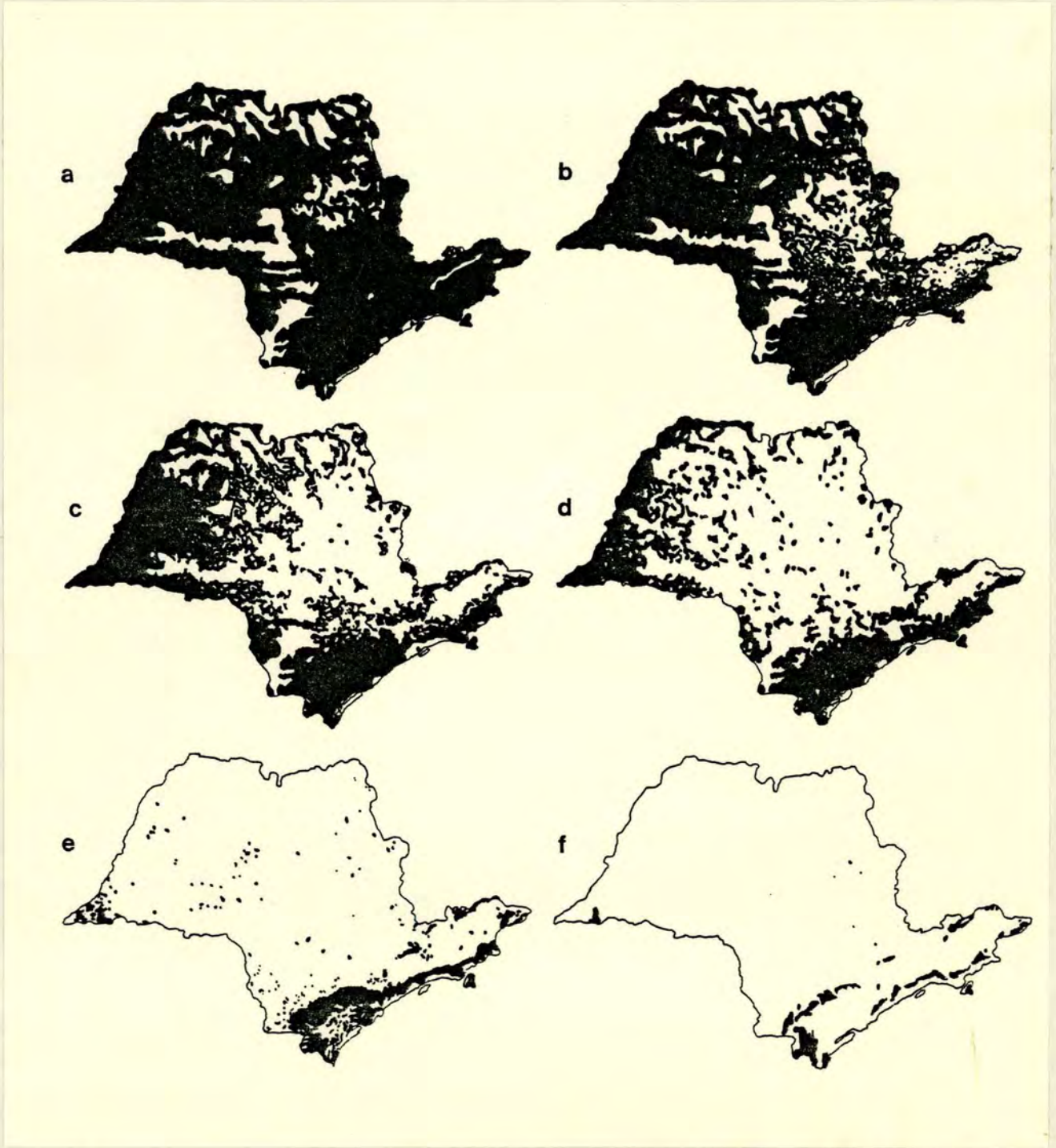
While detailed information is still wanting for most species, research has been stimulated by Brazilian organisations such as I.N.P.A. (Instituto Nacional de Pesquisas da Amazônia), I.B.D.F. (Instituto Brasileiro de Desenvolvimento Florestal) and the "Trópico Úmido" project, and it is to be expected that information on Amazonian primates will quickly increase in amount and quality.

Research in the Atlantic forest

The coastal areas of Brazil are much more developed than the interior. Such development has been, for more than four centuries, associated with the exploitation and destruction of the Atlantic forests. Most of the original vegetation has been removed. Only patches of forest are left. Fig.2 shows a representative example of the rate of deforestation.

The fact that the remnant forests are in developed areas should make them more accessible for field primatologists, but there is no tradition of sustained primate field work in this region. Most of the available information comes from short-term studies (see Table I.1 in section I.1.2) Although there are estimates of total population and detailed maps of present day distribution for some endangered species (e.g. Aguirre 1971 for Brachyteles, Coimbra-Filho & Mittermeier 1973, Coimbra-Filho 1976,1978 for Leontopithecus, Coimbra-Filho et al. 1981 for some Callithrix forms), there is almost no information on habitat usage either for these or for other primate species of the Atlantic region. Basic questions cannot still be answered. An indicative example is the much discussed case on the possible parapatry of some forms of the

Fig.2 - Map of São Paulo State, southeastern Brazil, showing the proportion of forest cover (dark areas) in the primitive situation (a), in 1886 (b), in 1920 (c), in 1952 (d), in 1973 (e) and in a prospect for 2000 (f). From Victor 1975.



Callithrix jacchus group (see Hershkovitz 1975,1977, Coimbra-Filho et al. 1981). A medium-term field project might have provided the decisive evidence a long time ago.

Some medium-term projects have been conducted recently (on Callithrix, Maier et al. 1982, Alonso, in prep.; on Callicebus, Kimura dos Reis, pers.comm..; this work). Unfortunately, field research in this region started very late. Human interference in the few remaining forested areas is often very intense, it is difficult to find a suitable site, and some topics are now very hard to investigate; for instance, are the primate densities presently observed in the remnant forests natural, or have they been altered by human interference? How do (did) Leontopithecus and Callithrix share resources? What was the original distribution of Leontopithecus races? Race studies in this area are also complicated by individuals from allien races being artificially introduced into remnant forests.

The contribution of this work

My original plan was to describe the behaviour of Cebus apella in a natural environment, and identify the most striking aspects of the interaction between Cebus and the habitat. Sympatric species would be observed only to the extent that they interacted with Cebus. The project was to be conducted in a forest of São Paulo State, Brazil, during a 12 to 15 months period. The project also included the examination of museum specimens of Cebus apella, in order to characterize the forms found in this part of the range, since the literature on this subject was unsatisfactory and no revision was being done at the time (P.Hershkovitz, pers.comm.,

P.Napier, pers.comm.)

When the work was planned, C.apella had not been the subject of sustained field work like that of Oppenheimer on C.capucinus (1968, 1969a,b,c, 1977). Most published information on C.apella was the by-product of studies on other species, and involved Amazonian races almost exclusively (e.g. Thorington 1967, Hernandez-Camacho and Cooper 1976, Struhsaker and Leland 1977, Izawa 1975,1976 etc.). Almost all the information on the Cebus of the Southeast was derived from epidemiological studies in the 1940's (e.g. Causey et al. 1948). Kuhlhorn (1939,1943a), Ruschi (1964) and Miranda Ribeiro (1924) also produced relevant field data, but these all came from short observations. C.apella was chosen as the study species because I had already studied it in captivity (Torres de Assumpção & Deag, 1979), and because its wide distribution should allow a greater choice of study sites.

The original plan could not be totally adhered to; financial restrictions forced me to stay in a site where the primates had been previously hunted; the primates did not habituate to being observed, which seriously affected data collection. Meanwhile, good quality observations had been made on Peruvian and Colombian Cebus apella (Janson, in prep.; Izawa 1978,1979,1980) and on Venezuelan Cebus nigrivittatus (Robinson, 1979,1980), and I decided to change the focus of the study. Instead of getting information on one species preferentially, I collected as much information as possible on all the species present at the site; these included the little known and endangered Brachyteles and Callithrix jacchus aurita. Although such a broad study (similar to that reported by Mittermeier and Roosmalen 1981) provides a good overall picture, it does so at the expense of

detail. Nevertheless, I believe that the collected information will be useful for the management of primates in this and other areas of the Atlantic domain.

The alteration of focus is reflected in the format of this dissertation: the first part refers to the use of a forest by its five primate species, and the second results from my original interest in Cebus apella - a reappraisal of its races, based on the examination of museum specimens and on field observations.

SECTION I

AN ECOLOGICAL STUDY OF PRIMATES AT A SITE IN SOUTHEAST BRAZIL

I.1 - Characteristics of Southeastern Brazil

I.1.1 - Environment

Brazil's most diversified relief is found in its southeastern region, where, after the Silurian period, the ancient Brazilian shield was bent and fractured, forming mountain ranges along the Atlantic coast. These mountains are now around 1200-1800m high (peaks reach 2900m). East of these mountains the rivers are short and flow directly into the Atlantic. To the West the rivers form larger systems (e.g. R.Paraná and R.São Francisco), and eventually also drain into the Atlantic. The western rivers helped form the western tablelands, presently 200 to 900m high. The tablelands can be divided into two sets: one of archeozoic/proterozoic crystalline rocks, and one of paleozoic and mesozoic sedimentary rocks. Most of S. Paulo State lies on the second type of tableland.

The characteristic climate for this tropical region involves the alternation of dry and rainy seasons. The rainfall is not homogeneously distributed over all the region. The eastern and southern sections, more exposed to the disturbed air systems from S and E, receive more rain. The interior receives less rain. In general, areas with lower rainfall have longer dry periods, but local relief alters this pattern: mountain ranges tend to shorten the dry period, while deep valleys do the opposite. The interaction between relief and climate produces quite a diversity of habitats in this region.

The vegetation of this region ranges from dry "caatinga" (thorny scrub) to hygrophilous forest (Fig.I.1) depending on the local soil type, relief and climate. At the same time, these variables are affected by the vegetation. In the coastal forests,

where the relative humidity is very high and the forest is evergreen, the soil is weathered mainly by chemical processes. This soil is quite different from that formed in the open vegetation areas where the weathering type varies with season (chemical alteration during the rainy season and mechanical disintegration during the dry season).

Because of the close interaction between the environmental variables, it is convenient to use the concept of morphoclimatic domains (Ab'Saber 1977a) to characterize this region's environment. A morphoclimatic domain is recognized by the superimposition of some typical geographical features of relief, climate, hydrology and vegetation. There are areas with a typical combination of these factors (core areas); core areas of different domains are separated by more or less broad transitional belts. In a core area a single vegetation type predominates, but enclaves of vegetation of other domains may be occasionally found.

A large part of the southeastern region belongs to the "tropical Atlantic domain", which is characterized by high humidity and rainfall, distinct dry and rainy seasons, chemically altered soils, hills shaped as half-oranges, typical vegetation being forest, and temperature varying according to latitude and altitude. Hygrophilous (evergreen) forest is found along the coast, and partially deciduous forest is found in the tablelands. It is mainly in the tropical Atlantic domain that primates are found.

Although the Southeastern region includes parts of three other domains (the "cerrado", the "caatinga" and the "Araucaria"), these have their core areas elsewhere, and the region contains only their edges. The "cerrado" core area is in central Brazil, the

Fig.I.1 - The original distribution of vegetation types in southeastern Brazil. The States of São Paulo (SP), Minas Gerais (MG), Espírito Santo (ES) and Rio de Janeiro (RJ) are shown. Prairies and Araucaria-mixed forests are only found in mountainous areas. Sea-side vegetation here refers to dune, mangrove and vegetation of shallows. Copied from Alonso (1977).


semi deciduous forest
evergreen coastal forest
deciduous non-thorny forest
occurrence of Araucaria
prairie
sea side vegetation
"caatinga"
"cerrado"
MG
ES
RJ
SP
0
200 km

"caatingas" typify Brazil's northeast, and the "Araucaria" forest is an offshoot of cold- climate Andean vegetation (Klein 1975). Full descriptions of these domains will not be given here (see Ab'Saber 1977 or Cerqueira-Silva 1980). It suffices to remember that both the "cerrado" and the "caatinga" domains are characterized by water deficit in the soil during the dry season, and that in both the vegetation does not form a closed canopy. Some primate species can be occasionally found in dense "cerrado", although they generally depend on the existence of a gallery forest nearby. They can also be found in "Araucaria" - mixed forests.

The environment described above corresponds to the primitive situation. Human activity has drastically altered the original landscape. Such alteration started in the XVI century with deforestation for agricultural purposes, and became particularly serious after the regional post-war urban/industrial boom. The population of this region, which was ca. 4,000,000 in 1872, went up to 40,300,000 in 1970. The region suffers from the joint effects of massive human population, heavy industrialization, poor planning and ineffectiveness of environmental protection. Some of the consequences include serious pollution, erosion and occasional landslides.

I.1.2 - Primates of Southeastern Brazil

The following primates occur in the Atlantic domain:

CALLITRICHIDAE

Leontopithecus rosalia rosalia
" " chrysomelas
" " chrysopygus (races as from Coimbra Filho and Mittermeier 1973)

Callithrix jacchus jacchus
" " aurita
" " flaviceps
" " geoffroyi
" " penicillata (races as from Hershkovitz 1977)

CEBIDAE

Callicebus personatus nigrifrons
" " melanochir
" " personatus (races as from Kinzey 1980)

Alouatta fusca
" caraya

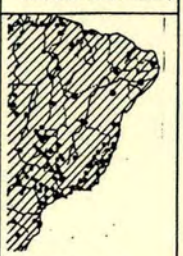
Brachyteles arachnoides (possibly two races)

Cebus apella (at least 3 races, and intermediate forms; see section II)

The status of the various species is mentioned in Table I.1, but such categorization is not completely satisfactory. For some species the taxonomic arrangement is confused or under revision so the conservation status of particular forms within those species tends to be neglected. For example, there are at least two forms of Cebus apella (xanthosternos Wied 1820 and robustus Wied 1820) which must be under serious pressure from habitat destruction, although the species as a whole is not endangered. Callicebus personatus personatus, with its restricted distribution, is probably also endangered. If Brachyteles arachnoides includes in fact two races, the northern one would be under the greatest pressure.

Another simplification is the inference of population sizes from distribution maps; most of them (including the ones in Table I.1) are made on the basis of museum material, and show the primates' original distribution, not the places where they presently occur. During my visit to several sites within the State of São

TABLE I.1
DISTRIBUTION AND STATUS OF SOUTHEASTERN BRAZILIAN PRIMATES.
(THE LATEST FIELD STUDIES ON EACH SPECIES ARE ALSO INDICATED)

SPECIES	LEONTOPITHECUS ROSALIA	BRACHYTELES ARACHNOIDES	CALLITHRIX JACCHUS	CALLICEBUS PERSONATUS	ALOUATTA FUSCA	CEBUS APELLA
STATUS	ENDANGERED	ENDANGERED	TWO FORMS ENDANGERED	VULNERABLE	INDETERMINATE	(not included in the Red Data Book)
DISTRIBUTION BEFORE HUMAN INTERFERENCE	 (from Coimbra Filho & Mittermeier 1973)	 (from Aguirre 1971)	 (from Kinzey 1980) [Shades = races] The two endang. ones in black	 (from Kinzey 1980)	 (from Kinzey 1980)	 (Shaded area = geographical distrib. Dots are localities where the species occurs (museum spec.)
LATEST FIELD STUDIES	-Coimbra Filho (1976,1978) (S) -Coimbra Filho & Mittermeier (1977) (S) (also U)	-Aguirre (1971)(S/M) -Milton* (S/M)(U) -Nishimura*(1979 & U)(S/M) -Torres de Assumpção (U & 1981)(M) -Valle (U)(M)	-Alonso**(U)(M) -Coimbra Filho et al(1981)(S) -Hubrecht** (U)(M) -Torres de Assumpção* (U)(M)	-Kimura dos Reis** (U)(M) -Kinzey & Becker** (U)(S) -Torres de Assumpção*(U)(M)	-Milton*(U)(S) -Silva*(1981)(S) -Torres de Assumpção*(U)(M)	-Takahashi**(U)(M) -Torres de Assumpção*(1981 & U)(M)
(M)-medium-term studies (at least 12 months in the site) (S/M)- interm. (3 to 12 m) (S)-short-term studies: (up to 3 m.)	General - Coimbra Filho, Mittermeier, Constable (U) (S/M)					
	(*) - quantified data (**) - detailed quantified data on known animals (U)- unpublished data					

Paulo, I found that some species were absent from forests where one would expect them to occur on the basis of distribution maps. In most cases it is difficult to discover whether a species has always been absent or whether it disappeared due to human activity. One example is the absence of Brachyteles, Alouatta and Callithrix from Gália (A in Fig. I.2), probably the largest remnant forest in the São Paulo tablelands (2000 ha in a single block). These primates had been recorded from within 100 km of Gália, in localities with the same habitat type (broadleaf semi-deciduous forest of the Paraná basin), the same climate (sub-hot with less than 3 dry months) and on geologic formations with the same origin (series Baurú and São Bento), therefore more likely to have similar soil and topography. The isolation of small populations in remnant forests may have led to the local extinction of species; however, the primate species absent in Gália are present at Barreiro Rico (B in Fig.I.2), in a smaller forest of the same general type.

It may be that, although the various remnant forests are of the same general type, they are not equally suitable to harbour primates. The primate density might always have differed greatly between localities. Species may have always been absent in particular areas. Heterogeneity in primate distribution may be associated with the recently revealed heterogeneity within the regional plant formations (Leitão Filho, pers.comm. based on studies of floristic composition of forest in São Paulo State).

It is also important to consider the primates' occasional dependence on localized resources which may or not have been preserved in the various remnant patches. For instance, a small area of Barreiro Rico forest, which does not look strikingly different from the rest,

constitutes a separate sub-habitat, with its own plant composition and structure; this area is important for primate feeding during part of the year (see section I.4). Only detailed ecological research in each forest might suggest the reasons why their primate populations differ.

Primate density seems to vary widely between localities. When visiting sites in the coastal pluvial forest (Boracéia, Carlos Botelho - E and F in Fig.I.2), I noticed that primates were very infrequently heard or seen, as compared to encounter frequency at sites in the tablelands (Ourinhos, Barreiro Rico, Gália - C,B and A in Fig.I.2). Although I did not conduct a detailed quantitative comparison, my impression is that primate density is much lower in the coastal forest. This could be due to a different carrying capacity in the two types of forest. It could also be that the present density is artificially high in the generally smaller and more affected tableland forests, which are often next to easy to raid orchard and plantations, and whose primates are occasionally fed by the farmers. Also, recent removal of forest parts may have forced many animals into the remnant patches, keeping the population at maximum density.

The choice of the intensive study site among the ones I visited was done on the basis of logistic facilities and primate diversity. Barreiro Rico is one of the last refuges of Brachyteles in the tablelands, and is the Southeastern Brazilian site with the highest primate diversity that I know.

Fig.I.2 - Map of São Paulo State, showing the primate species present in each site I visited. To facilitate visual comparison of the composition in different sites, all the six species have been included in each circle - even though sites might be outside the known geographical range of some species. Sites are:

A - Gália Reserve
B - Barreiro Rico Farm (south of Santa Maria da Serra)
C - Lajeadinho Farm (Ourinhos)
D - Cantareira Reserve
E - Boracéia Reserve
F - Carlos Botelho Reserve
G - Taurus Farm (southwest of Eldorado)
H - Juréia Reserve
I - Juquitiba (70 km southwest of São Paulo city)
J - Monte Mel Farm (70 km north of São Paulo city)
K - Parque do Estado Reserve
L - Paranapiacaba Reserve
M - Taiaçupeba (northeast of Paranapiacaba)
N - Ilha Grande (Rio de Janeiro State)

I.2 Characteristics of Barreiro Rico site

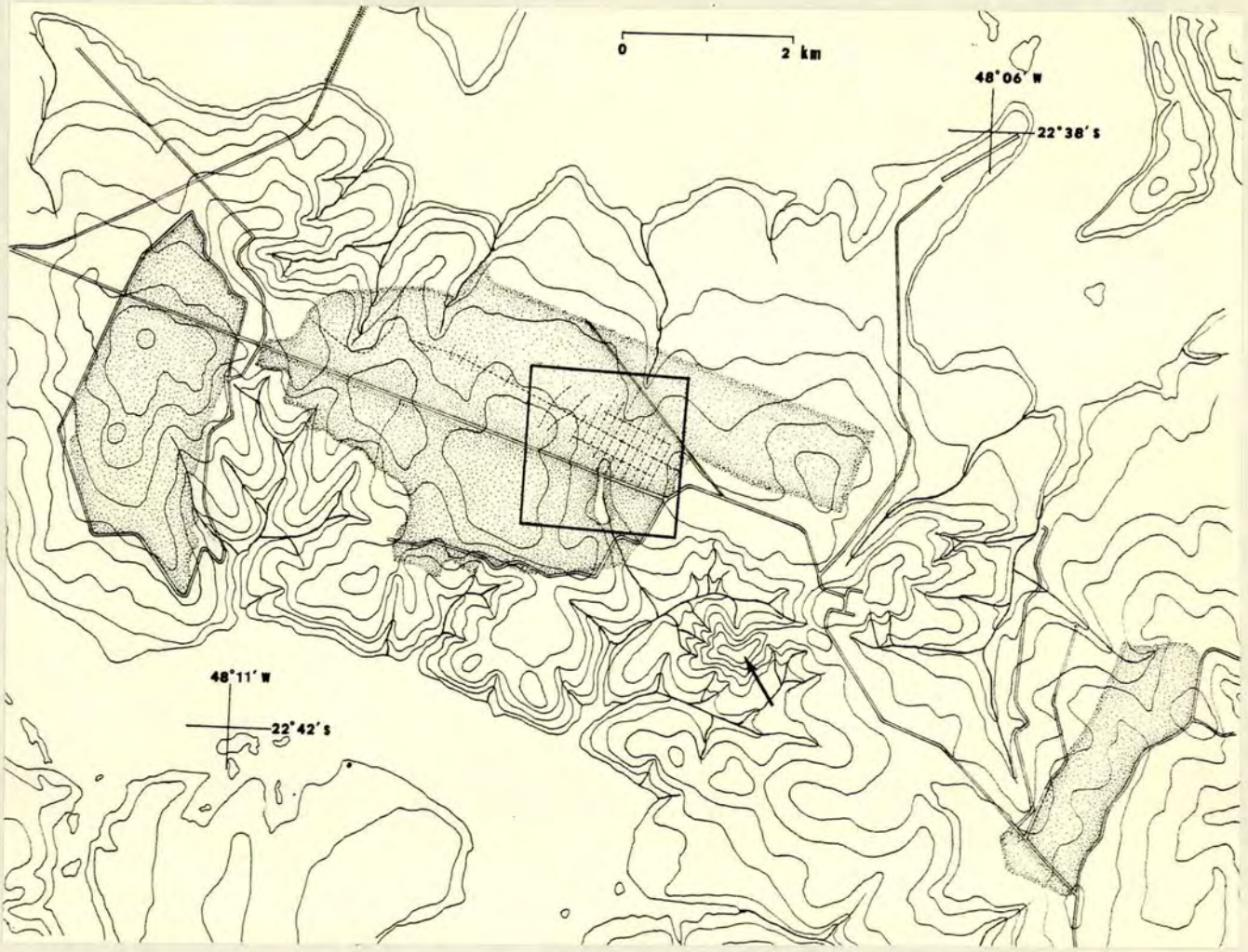
I.2.1 General information

The Barreiro Rico study site (referred to as B.R. in the text) is located in a privately owned farm in the central tablelands of Sao Paulo State. The terrain is fairly flat with altitude around 500m. Barreiro Rico includes some of the last tracts of original tableland vegetation in the State of São Paulo. The plots of original vegetation at B.R. measure 326, 488 and 1386 hectares, and include mainly woodland, but also a patch of "cerrado". The two larger remnant forest blocks are crossed by roads above which the canopy is broken: this restricts the free movement of canopy-loving species such as Brachyteles and Alouatta, and one may consider the forest to be in fact divided into six blocks. The location of these forest blocks is indicated in Fig.I.3. Although the area is at the junction of rivers Tietê and Piracicaba, the riverine forest does not exist any longer. Part of it was covered by water when the Barra Bonita reservoir was filled, and the rest was cut down.

I.2.2 Climate

The climate of this region is CwA in Koeppen's system - a fairly hot and humid climate. The annual rainfall is around 1300 mm/year. As the rainfall exceeds the evapotranspiration, a downwards flux of water is formed which leaches the soil (Setzer 1966). The months with the lowest rainfall are July/August (average for 19 years: 69mm for July and August considered together). The highest rainfall happens in December/ January, the hottest months (411mm for these two months together - average for 19 years). The largest differences between the average rainfall of two consecutive months occur between March and April (decrease in rainfall) and

Fig.I.3 - Location of woodland plots at Barreiro Rico (stippled areas). The square indicates the area pictured in Fig.I.5. Dotted lines are trails. The difference between contour lines is 20m. The arrow indicates the area of the diabase extrusion mentioned in section I.2.4. Based on the 1974 map published by the Instituto Brasileiro de Geografia e Estatística, Brazil (1:50,000, sheet Santa Maria da Serra).



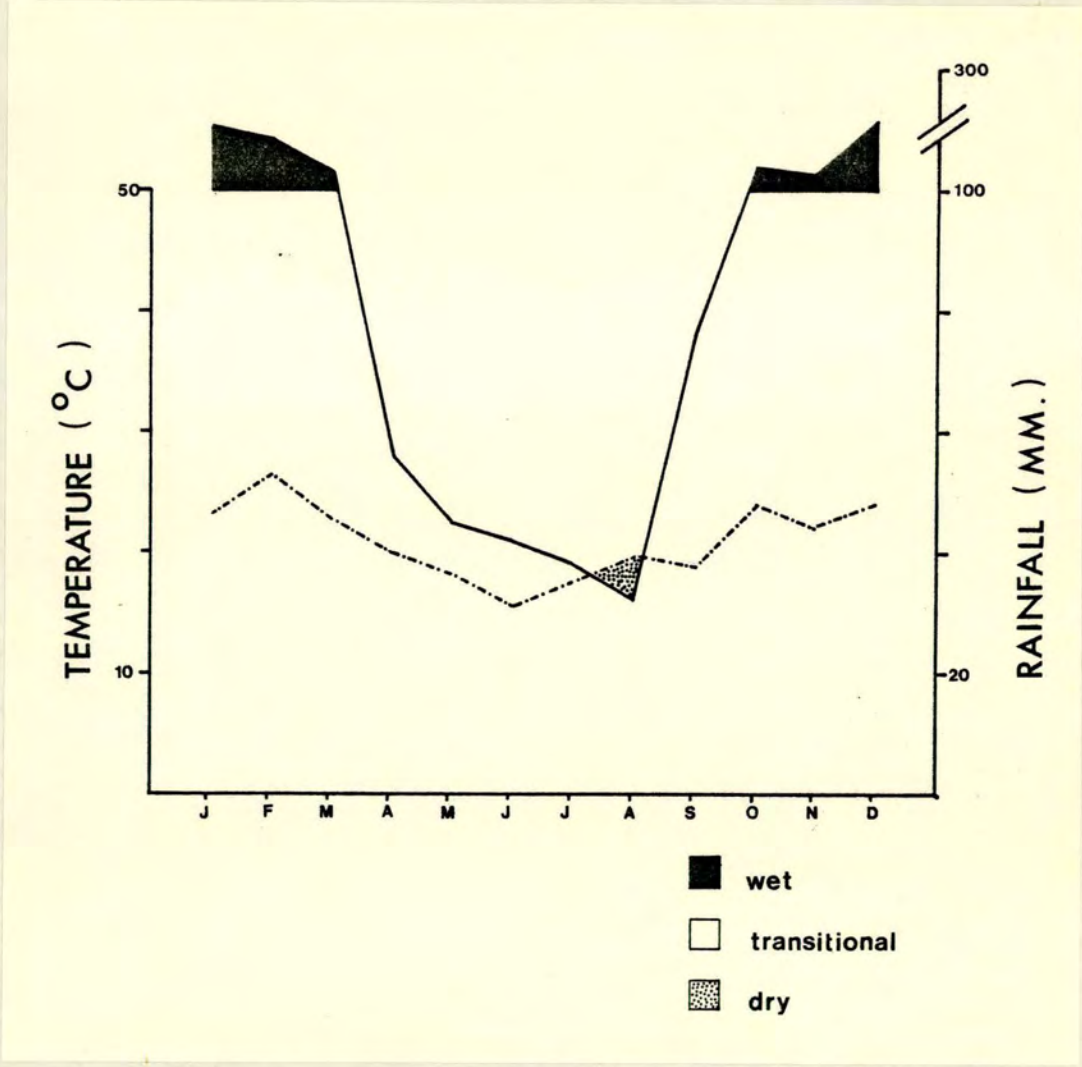
between September and October (increase in rainfall) (SÃO PAULO, 1972). Monteiro (1976) describes the climate of B.R. area in the following way: annual average temperature between 18 and 22 degrees Celsius, average relative humidity between 70 and 75%, existence of a dry season, during which there is no water deficit. Fig.I.4 gives a climatic diagram for Barreiro Rico.

I.2.3 Soil

In the central tablelands of São Paulo State the soil is a mosaic of very poor soil, very rich red soil and mixtures of both. These soils have their origin in a geologic formation ("Serie São Bento") which includes both sedimentary (sandstones) and magmatic (diabase,basaltite) rocks. These date from the Triassic, when lavas spread over the existing wind-produced desert. The layers of diabase and sandstones are quite flat. Erosion since the Cretaceous altered the original landscape and left some small hills emerging from the generally flat terrain. The hills may be of volcanic rock, but they can also show the typical succession of magmatic and sedimentary layers.

These two types of rock produced the soils we now find in the area. The sandstones, being almost pure quartz, formed a coarsely grained sandy soil with less than 5% of clay. This soil has a capacity for water retention of less than 10%, an extremely low amount of organic matter, no cohesion and low porosity; it is one of the worst soils for agriculture. According to Setzer (1942, p.292), if it were not for the favourable climate in this part of the State, the areas with this type of soil would be deserts. On the other hand, the magmatic rocks formed chemically rich, porous soil with

Fig.I.4 - Climatic diagram for Barreiro Rico, using the representation method of Walter and Leith (1967) as described in Eisenberg et al. (1981). The rainfall data are averages for 19 years (Barreiro Rico rain gauge). Temperature data come from a single year (1979). The indicated temperatures are the averages between minimum and maximum temperatures as from circa 10 readings/month. The thermometer was in a shaded place in the forest (1.5 m above the ground).



high water capacity (up to 45%). This soil is one of the best for agriculture and has always been intensively exploited.

The soil map of B.R. (Ranzani and Pessotti (1975), shows all tracts of forest to be on quartz sand; this type of soil can be, according to Setzer (1942), dozens of meters deep. Data on the vegetation cover of B.R. collected during this study suggest that the soil may not be homogeneous in all the forested area (see section I.2.4), but no detailed soil study is available.

I.2.4 Vegetation

According to Setzer (1942, p.276) the primary vegetation of the poor sandy soils mentioned in the previous section is a not too dense "cerrado" containing drought-resistant species; trees in this habitat rarely grow beyond 5m and are usually less than 10cm diameter at breast height (d.b.h.). The vegetation of the rich soils is high forest (tree height around 20-30m and d.b.h. up to 2m). In the intermediate types of soil the vegetation varies from "cerradão" (dense tall "cerrado") to forests with some xerophytous elements. Trees in the intermediate soil rarely exceed 1m d.b.h. On the basis of this description, the sandy soil of B.R. forest would be classified as "intermediate". Some views of B.R. vegetation are shown in Fig.I.6. Willis (1979) described the forest of B.R. as "less developed" than remnant forests on red rich soil. He considered this normal because "Barreiro Rico lies on an ecotone near areas of cerrado and cerradao" (p.4). Willis' statement suggested that there is an exuberance gradient associated with soil type, but it also implied that ecotones spread over large areas, the transition from one vegetation type to another being gradual. This

does not seem to be the case in B.R., where sharp boundaries can be seen between cerrado and forest. It seems that in this region the vegetation is an indicator of the quality of the soil immediately below, and that the soil may change quite abruptly. There are several indications of this at B.R.:

a. The farm contains a patch of soil which originated from a diabase extrusion (topographically this is now a round-top hill - see arrow in Fig.I.3). The original vegetation of this hill has been removed, but farm employees who are familiar with the local plant species state that the forest on such "good soil" (their term) included several species not found elsewhere in the farm.

b. There is a patch of "cerrado" in the middle of a woodland plot at B.R. (see Fig.I.5), and the sandy soil of this area is particularly deep (J.C.R.Magalhães, pers.comm.). This "cerrado" fits Setzer's (1942) description of the poor sandy soils vegetation.

c. There is an association between relief and different types of forest at B.R.; this may be due to different soil qualities, associated with different rock foundations. The hills possibly contain a higher proportion of the richer and more resistant diabase. These different types of forest are not a direct product of the (slight) difference in altitude, since more than one type of forest can be found at the same altitude, at B.R.

There are few streams in B.R. woods; near them selective species are found. It may be that the forest along streams is reminiscent of the riverine vegetation that has been covered by the dam. Such vegetation included species not encountered in the remaining patches (J.C.R.Magalhães, pers.comm.). Unfortunately, neither the riverine forest nor the "good-soil" forest were

Fig.I.5 - Aerial photograph of the intensive study area - this area corresponds to the square in Fig.I.3. Segments a, b and c indicate the location of the transects mentioned in the text. Dotted lines are trails. Note the area of open vegetation, clearly distinguished from the forest.

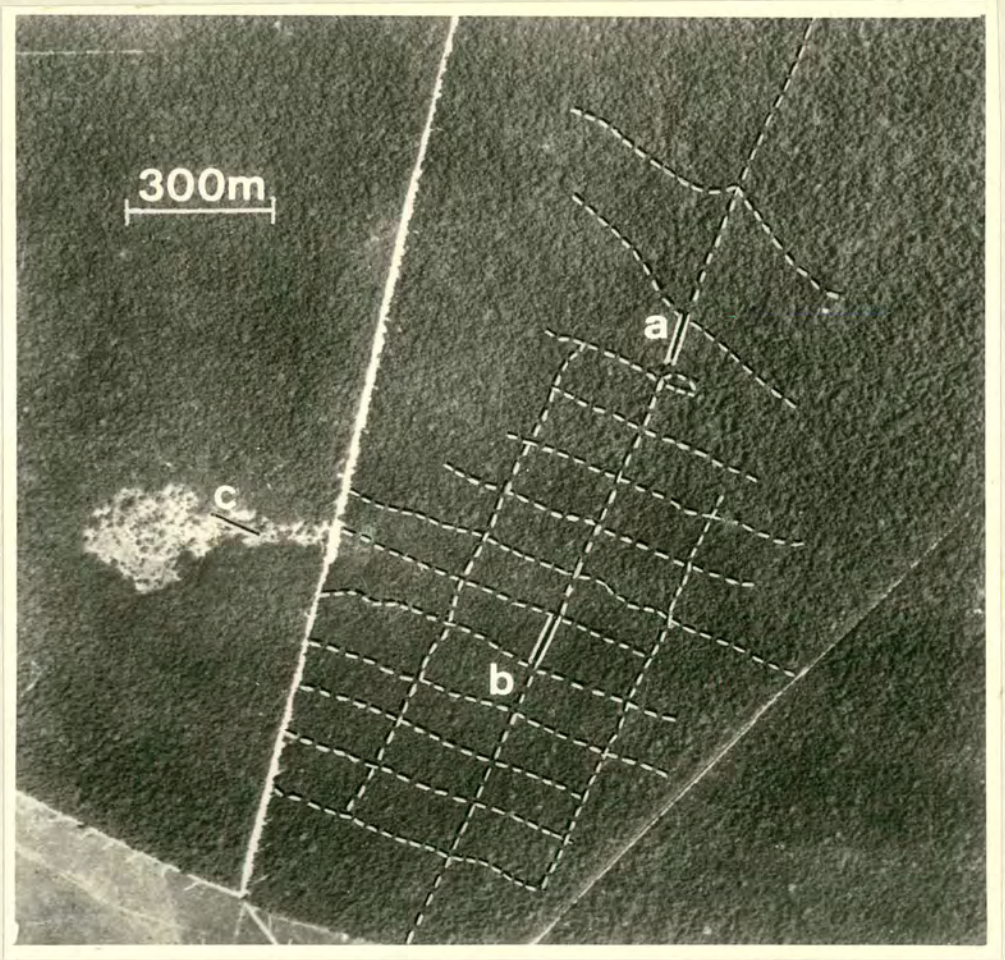
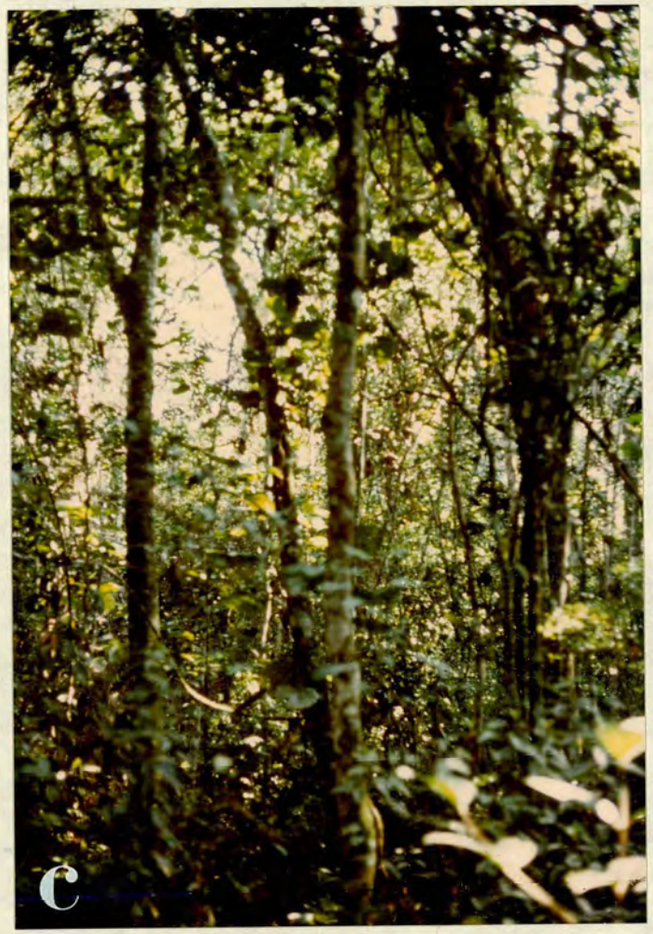


Fig.I.6 - Views of the study area.

a. interface pasture land/forest
b. trail in a moderately dense part of the forest (*)
c. the forest in its least dense aspect (*)
d. area "c" (refer to Fig.I.5)

(*) - The aspect of the forest shown in these pictures did not change between seasons; the deciduous species (most of them tall trees) were generally spaced out and their lack of leaves did not really affect the light intensity at ground level.



systematically studied before being destroyed. This study constitutes the first documentation of the remaining vegetation. Most of the information comes from a 115-ha intensive study area, but some samples were collected outside that area. Only condensed results will be presented here. More extensive discussion can be found in Torres de Assumpção et al. (1982), included here as Appendix I.6.

I tried to obtain samples from all plant species when they were seen to flower or fruit. This procedure was maintained for more than 12 months, so all species which flower annually could in principle have been sampled. However, some did not flower and I was unable to get a suitable sample from others.

I tagged and plotted up to 15 individuals of each recognized species. The tagged individuals provided part of the phenology data, and helped to locate sub-habitats.

Between Jan/79 and Jan/80 I sampled 158 angiosperm species from 55 families; 76 were trees, 38 shrubs, 21 lianas, 16 herbs and 7 epiphytes. The sampled species are listed in Appendix I.1. The tree component seems to have been sufficiently sampled; I compared my list of woody species with the list of B.R. woods (based on B.R. owners' private collection) and found that the 10 species that were missing from my list correspond to species typically found in pasture land or in good-quality soil, therefore unlikely to be found in my intensive study area. (These species are not included in Appendix I.1).

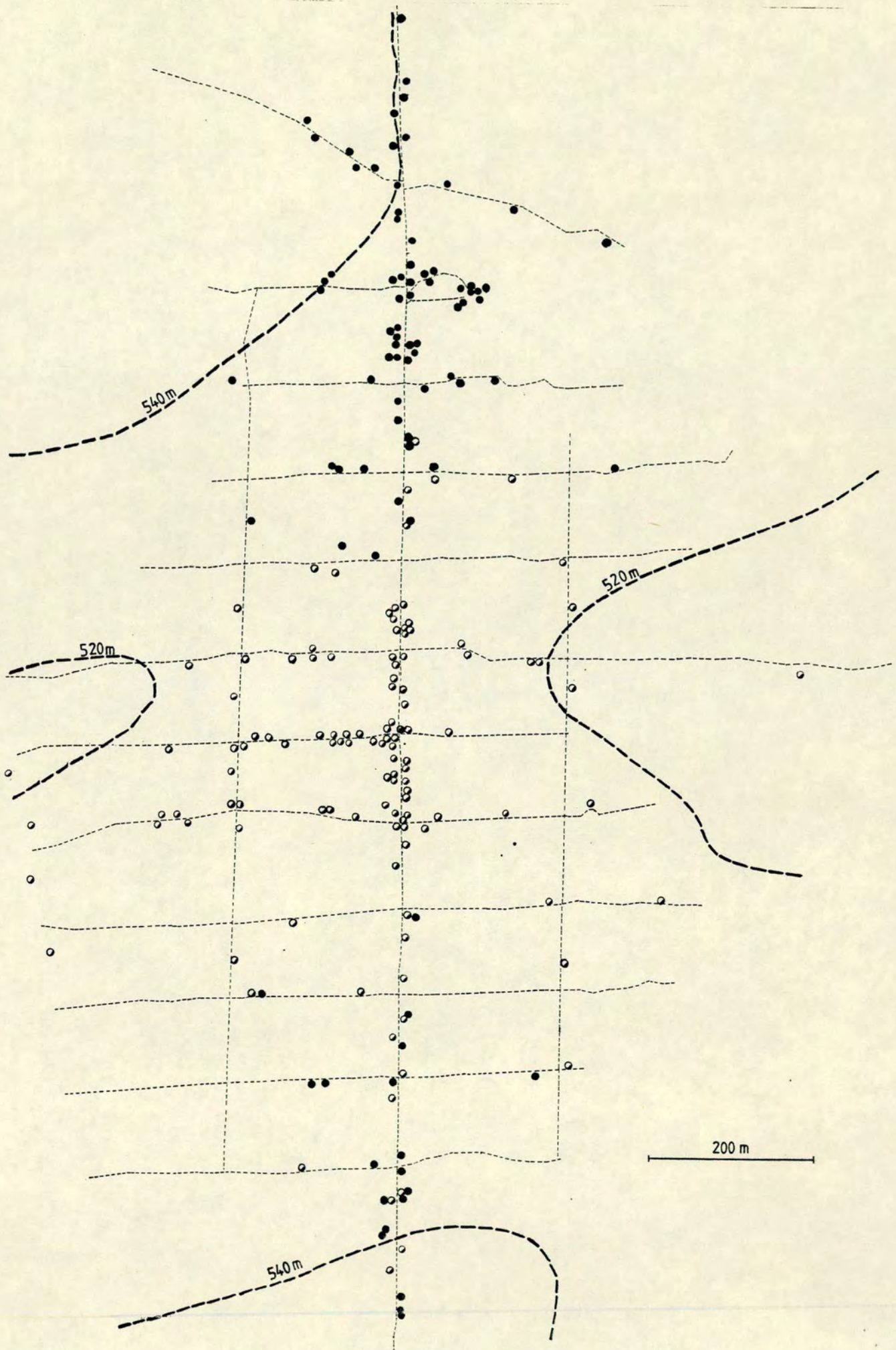
Since the tree component of B.R. seems to be adequately sampled, I compared its floristic composition to that of other South American forests. The highest affinity is, as expected, between

Fig.I.7 - The location of tagged individuals of selective and exclusive species in the forest of Barreiro Rico. Each circle is one individual. Only trees and shrubs are considered.

Dark circles: species which identify sub-habitat "A"

Empty circles: species which identify sub-habitat "B"

(Obs.: sub-habitat "C" is the open vegetation enclave mentioned in Fig.I.5; this area is not included in this figure)


540 m
520 m
520 m
200 m
540 m

B.R. and other forests of the R.Paraná formation. The next most similar forests are, in decreasing order of affinity: Atlantic coastal forests, east Amazonian forests, central Brazil gallery forest, central Amazonian forests, and with least affinity, the forests in West Amazonia and Panama (Torres de Assumpção et al., 1982).

Not all plant species are homogeneously distributed in the forest. Some are more frequent in particular areas (selective species), and some (estenotopic or exclusive species) can only be found in particular areas. Selective and exclusive species are listed as "non-indifferent" in Table I.2, and they characterize the three sub-habitats of the study area. Two of these ("A" and "B") are forest- like; the third ("C") is physiognomically similar to a "cerrado", being readily distinguishable in an aerial photograph (Fig. I.5). The distinction between "B" and "A" is not so clear. It can be shown by plotting the individuals of selective and exclusive plant species on a map (Fig. I.7).

A restricted sample suggests that each of these three habitats has its own predominant plant families (Table I.3), its own structure (Fig. I.8) and may follow its own phenological timing (Table I.4).

"B" is located between "A" and "C" and, like "C", covers a restricted area. However, "B" does not seem to be an ecotone between "A" and "C". Many of the species found in "B" are exclusive to it, and those typically found in "A" and "C" do not mix in the area of "B". Neither in diversity or density is "B" a transition between the other two habitats. "B" has the highest diversity and density of all the three environments (Table I.3), whereas "C" is

TABLE I.2
EXAMPLES OF INDIFFERENT AND NON-INDIFFERENT PLANT SPECIES.
"NON-INDIFFERENT" SPECIES CAN BE EITHER SELECTIVE OR EXCLUSIVE.

SUB-HABITAT	NON INDIFFERENT SPECIES	INDIFFERENT SPECIES
A + B		Aspidosperma nemorale (Apocyn.) Gonatogyne brasiliensis (Euphorb.) Actinostemon estrellensis (Euphorb.) Alchornea triplinervia (Euphorb.) Cryptocarya moschata (Laur.) Ocotea acutifolia (Laur.) Hymenaea courbaril (Legum.) Qualea jundiahy (Vochys.)
A+B+C		Copaifera langsdorfii (Legum.)
A (*)	Aspidosperma peroba (Apocyn.) Securinega guaraiuva (Euphorb.) Nectandra sp.(canela-cheirosa)(Laur.) Zollernia ilicifolia (Legum.) Pachystroma illicifolium (Euphorb.) Callyptrogenia sp.(piuna)(Myrt.) Psychotria sp.(7565)(Rub.) Esenbeckia leiocarpa (Rut.) Pilocarpus pauciflorus (Rut.) Galipea jasminiflora (Rut.) Metrodorea nigra (Rut.)	
B (**)	Annona cacans (Annon.) Duguetia lanceolata (Annon.) Cordia sellowiana (Borag.) Maytenus sp.(7571)(Myrt.) Mabea fistulifera (Euphorb.) Pera obovata (Euphorb.) Miconia candolleana (Melast.) Eugenia sp.(7517) Psidium sp.(7546)(Myrt.) Myrcia formosiana (7520)(Myrt.) Amaioua guyanensis (Rub.)	
C	Duguetia furfuracea (Annon.) Didymopanax vinosum (Aral.) Ocotea pulchela (Laur.) Stryphnodendron adstringens (Legum.) Byrsonima campestre (Malp.) Byrsonima intermedia (Malp.) Miconia fallax (Melast.) Rapanea lancifolia (Myrs.) Myrcia spp.(7574,7576)(Myrt.) Blepharocalyx sp.(Myrt.) ?Campomanesia sp. (7578)(Myrt.)	

(*) Maybe also Mouriri sp (7521),Miconia sp (7552),Astronium graveolens, Coccoloba sp (7579) and Zanthoxilum rhoifolium.
(**) Maybe also Gomidesia sp (7524), Inga striata and Guazuma ulmifolia

TABLE I.3
COMPARISON OF THE TRANSECTS' FLORISTIC COMPOSITION
(see Fig. I.5 for transect location and Fig. I.7 for forest structure)

SUB-HABIT.	COMMONEST FAMILIES	% OF TOTAL N. INDIVIDUALS IN TRANSECT (*)	SPP INVOLVED	SPECIES IN TRANSECT	N.SPECIES / N.INDIVID.
A	Rutac.	15/29=52%	Esenbeckia leiocarpa Pilocarpus pauciflorus Metrodorea nigra Galipea jasminiflora	12	0.41
	Melast.	05/29=17%	Mouriri sp. (7521)		
B	Euphor.	18/38=47%	Mabea fistulifera Aparisthmium cordatum Croton floribundus Gonatogyne brasiliensis	20	0.53
	Myrt.	06/38=16%	Gomidesia sp.1 (7524) Gomidesia sp.2 (7530) Myrcia formosiana Eugenia sp. (7517) Myrciaria sp. (7532)		
C	Legum.	06/14=43%	Stryphnodendron adstringens Copaifera langsdorfii	07	0.50
	Myrt.	04/14=29%	Blepharocalyx sp. Myrcia spp. (7575,7574)		

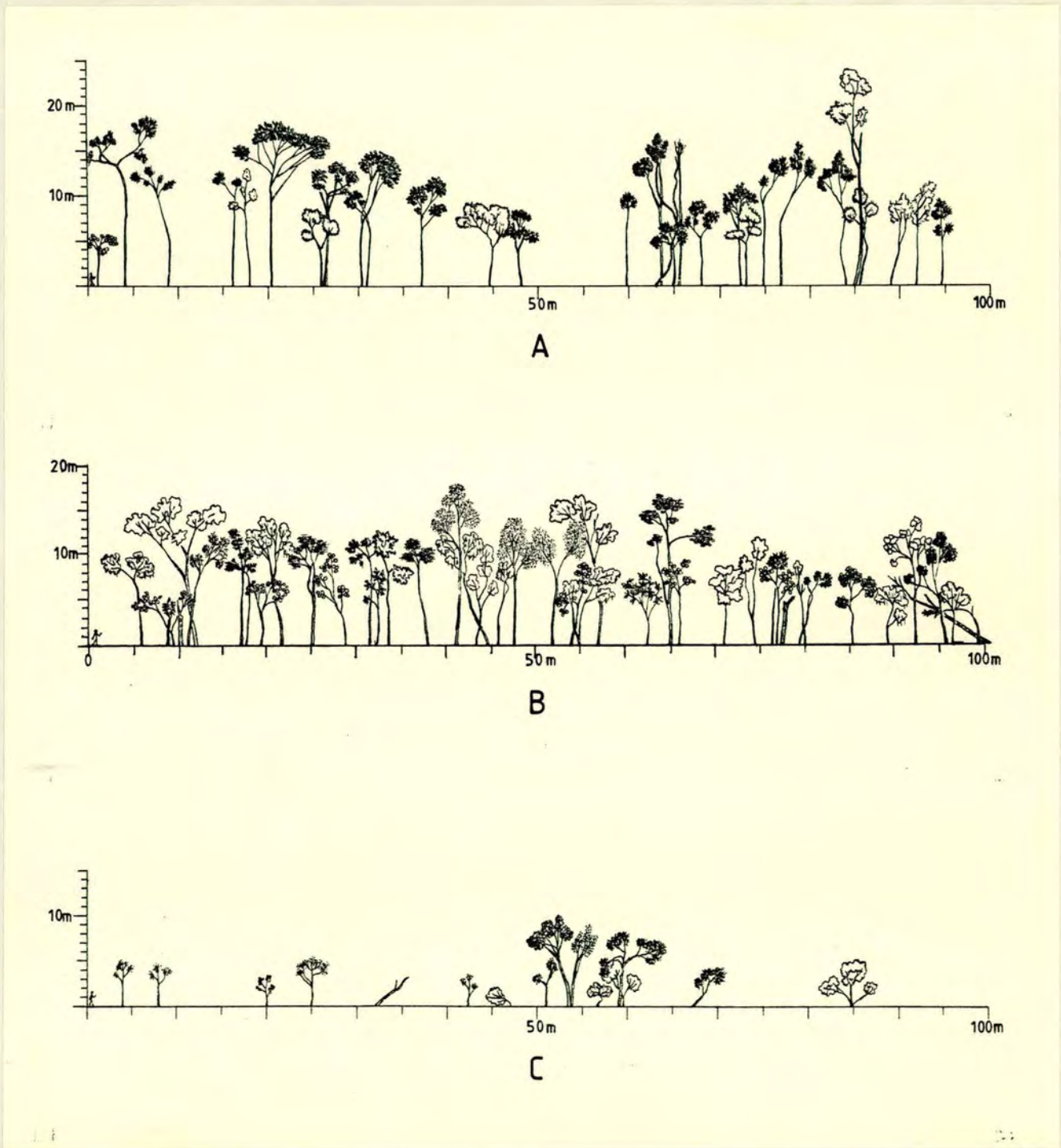
(*) fIG.I.5

TABLE I.4
FLOWERING THROUGH THE YEAR

In each cell it is indicated the number of species observed to be flowering. Values in a circle are significantly above (two standard deviations) the row average. Question marks indicate the cases for which there is no information (in these cases the value is probably similar to zero). Brackets are used for the cases in which the information does not come from direct observation (e.g., information given by local people).

Month / Spp.from sub habitat	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
A	2	3	1	0	0	2	2	1	(6)	3	2	2	22
B	2	2	3	1	3	1	0	3	5	(8)	2	1	29
C	0	0	0	0	2	?	0	0	?	(5)	0	1	8
Indif. spp	0	0	1	1	(1)	0	0	1	5	5	3	3	20

Fig.I.8 - Profiles of vegetation in the three 2.5 x 100m transects of Fig.I.5. For "A" and "B" all plants with at least 10 cm D.B.H. are drawn. In "C", most species branch near the soil, so the profile includes the plants with at least 10 cm diameter at any height.



the poorest. The vegetation of "C" is probably the response to a very hostile environment. Even those plant species which occur in all three habitats do not reach, in "C", the same size that they reach in the others. The few trees present in "C" are clumped and shaped in a way that suggests competition for soil patches. Although soil is probably the most important factor in the distinction of these habitats, at least three others could be also involved: frosts (which affect mainly the lower areas), fire (at least one occurred in the area of "B") and depth of the watertable (possibly associated with the relief).

I.2.5 - Seasonality

At B.R. seasonality is clearly linked with rainfall. Although water deficit may not be serious every year, it probably is a limiting factor (see Fig.I.4). In the years when rainfall is low or rains are late (e.g. 1981) treelets and vines may show flaccid leaves or tilting branches. The fact that the forest is semidecidous also indicates that water stress is not negligible; many of the large common trees (e.g. Hymenaea courbaril, Copaifera langsdorfii, Aspidosperma nemorale, Astronium graveolens) shed their leaves during the dry season. The shedding of leaves is reflected in a strong increase in litter production at the end of the dry season (August and September) when the water deficit is more likely to be serious. Fig.I.9 shows the seasonal changes in litter production.

I did not measure relative humidity in the forest, except for a few days each month, when I took one reading/day during the hottest hours (generally between 11h30 and 15h00). This aimed at

estimating the minimum humidity faced by the primates (although the measurements were taken near the forest floor). The lowest reading was 48%; monthly averages for the hottest hours oscillated between 60 and 90% (see Fig. I.9b).

Most plant species flower or fruit with the onset of the rains; for many the production of any reproductive structure is restricted to the rainy season (Tables I.4 and I.5). Some species (e.g. Xylopia brasiliensis and Qualea jundiahy) may flower during the dry period but seem to delay fruit maturation until the following rainy season. Fleshy fruits are rare during the dry season; most species fruiting during this period produce woody dehiscent fruit.

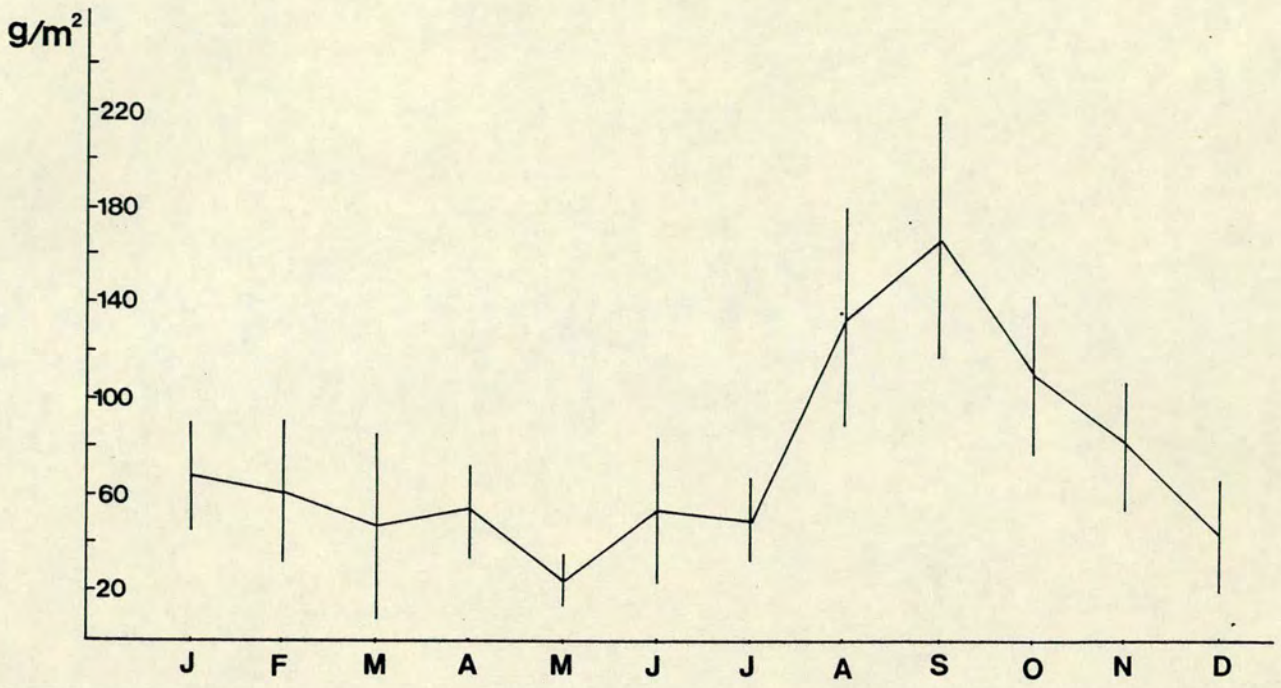
The rainy season is also the time when most birds and mammals produce their young (see Table I.9 for data on mammals). Many animals in the area do not have access to running water and have to rely on rain or on water-rich food, both scarce during the dry months. It may be impossible for these species to rear young during the dry period.

The seasonality also shows in the abundance of particular invertebrates. For instance, the younger stages of ticks (probably Ornythodorus molbata) are extremely abundant from March through June (perhaps associated with the reproduction of the peccaries they are said to parasitise). Wingless forms of termites (samples in S.Paulo Museum) were observed changing nests in February , April and May, but winged forms emerged only during an unusually rainy August and then (and mainly) in October. Winged forms of ants (Atta sp) (samples in S.Paulo Museum) emerged from September through November. Solitary wasps were particularly abundant at open areas in October.

Fig.I.9 -

a) Monthly litter production at Barreiro Rico. Data from O.Cesar, in prep. The area sampled by O.Cesar corresponds to habitat "A" almost exclusively.
Litter production at B.R. is around 9150 kg dry weight per hectare per year (O.Cesar, in prep.), a value that exceeds the figures quoted by Hladik (1978) for montane evergreen forest (India, Sri Lanka), temperate deciduous or temperate evergreen forest (France), and is in the range of tropical forest, either semideciduous or evergreen, at Ghana, Panama, Malaya and Ivory Coast.

b) Relative humidity in B.R. forest during the hottest hours (details in the text). The dotted lines indicate the 1 st.dev. confidence limit. Data collected in 1979.


g/m²
220
180
140
100
60
20
J
F
M
A
M
J
J
A
S
O
N
D

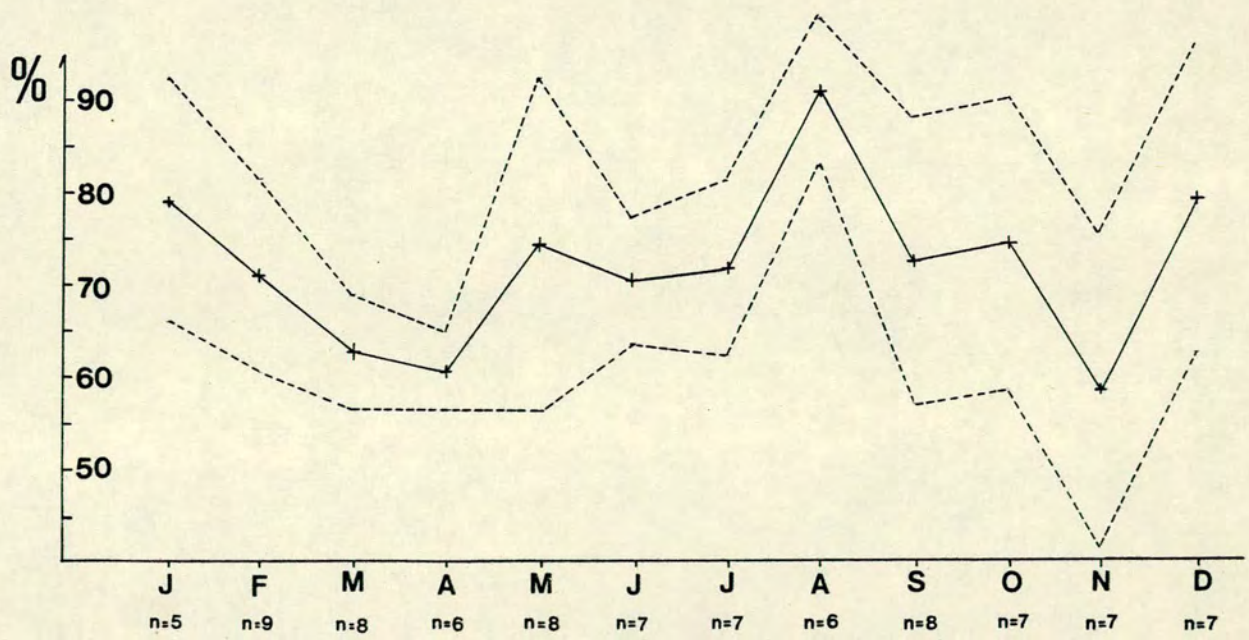

%
90
80
70
60
50
J
n=5
F
n=9
M
n=8
A
n=6
M
n=8
J
n=7
J
n=7
A
n=6
S
n=8
O
n=7
N
n=7
D
n=7

TABLE I.5

THE PRODUCTION OF REPRODUCTIVE STRUCTURES THROUGH THE YEAR (ONLY TREE SPECIES)

Brackets are used when the information was not taken from field notes (it is only a logic link between data of adjacent months). Blank cells do not indicate lack of observations, but the non-existence of reproductive structures.

FT - ripe fruit;
ft - immature fruit;
FL - open flowers;
fl - immature flowers;

SPECIES	MONTHS											
	J	F	M	A	M	J	J	A	S	O	N	D
Esenbeckia leiocarpa		ft	ft	(ft)	ft	(ft)	FT	FT	FT	fl	FL	FL
Cryptocarya moschata	FT	FT	FT						fl	(fl)	ft	FT
Annona cacans	FT	FT							FL	FL	ft	ft
Croton floribundus	FT	FT								FL	ft	FT
Securinega guaraiuva	(ft)	(ft)	FT	FT		FT	FT		FL	ft	ft	ft
Gonatogyne brasiliensis	FT	FT	FT				fl	(fl)	FL	FL	ft	FT
Pilocarpus pauciflorus		FL	FL	(ft)	(ft)	ft	(ft)	(ft)	ft			
Galipea jasminiflora	FL	FL	(ft)	ft	ft	FT						fl
Vochysia tucanorum	FL	FL	FL		FL			ft				fl
Mabea fistulifera	fl	FL	FL	FL	FL	ft	ft	ft	FT	FT		
Eugenia sp. (am.7517)	ft	FT	FT									?fl
Myrcia formosiana	ft	FT								fl	FL	ft
Mouriri sp. (am.7521)		ft		ft	ft	ft		ft	FT	FT		?fl
Qualea jundiahy	(ft)	(ft)	ft	(ft)	ft	(ft)	ft	(ft)	FT	FL	FL	(ft)
Gomidesia sp. (am.7524)	(ft)	(ft)	FT								FL	(ft)
Pera obovata			FL		FL		ft	ft	FT	(FT)	FT	
Alchornea triplinervia			FL		ft					ft	FT	FT
Ocotea aff. spixiana				FL	FL	ft	(ft)	FT	FT	FT	FT	
Hymenaea courbaril				ft	ft	ft	FT	FT	fl	FL		
Ilex cerasifolia			ft	(ft)	(ft)	FT				FL		
Myrciaria sp. (am.7532)												fl
Aparisthmium cordatum	FT									FL	ft	FT
Cordia sellowiana				ft	FL ft							
Sloanea monosperma						ft	ft	FT	FT			
Copaifera langsdorfii	(ft)	(ft)	(ft)	(ft)	ft	FT	FT	FT				FL
Psidium sp. (am.7546)						FT	FT	FT fl				ft
Agonandra brasiliensis							FL					
Duguetia lanceolata	ft	FT					fl	(fl)	FL	FL		ft
Metrodorea nigra	(ft)	FT					fl	fl	FL	(ft)	(ft)	(ft)
Miconia sp.(7552)		fl					FT	FT				
Astronium graveolens								FL	FL ft	ft	ft	
Eugenia pyriformis									FL FT	FT		
Callyptrogenia sp.									FL			
Aspidosperma nemorale									FL	(ft)	ft	FT
Villaresia sp.									FT			
Xylopia brasiliensis									FT fl	FT FL	FL	FL
Maytenus sp. (am.7571)										FL	(ft)	ft
Ouratea salicifolia										FL	(ft)	ft
Coccoloba sp. (7579)										FL	ft	ft
Amaioua guianensis											FL	
Zollernia ilicifolia										FL	FT	
Ocotea acutifolia											fl	FL
Didymopanax morototoni	FL ft									fl	(fl)	FL ft
Inga striata	ft	FT						fl	FL	FL	(ft)	FT
Aspidosperma peroba	ft	(ft)									FL ft	ft
Pachistroma illicifolium	ft	FT								fl		
Esenbeckia intermedia	FT											FL
Psychotria sp. (am.7565)	FT	FT							FL	(ft)	ft	FT

TABLE I.6
TIME SPENT OBSERVING PRIMATES IN DIFFERENT SEASONS (1979)

SPECIES	RAINY SEASON (October through March)		DRY SEASON (April through September)	
	Number of encounters (*)	Time spent observing	Number of encounters (*)	Time spent observing
CALLICEBUS	11	2 h 38	4	0 h 40
	Vocalization bouts heard: 58		Vocalization bouts heard: 53	
CALLITHRIX	18 (21)	6 h 13	22 (23)	5 h 52
BRACHYTELES	21 (24)	15 h 56	10 (14)	6 h 44
CEBUS	98 (108)	96 h 49	151 (164)	177 h 03
ALOUATTA	20	18 h 21	18	7 h 44
	Vocalization bouts heard: 40		Vocalization bouts heard: 50	

(*) Values outside brackets are the number of encounters which involved at least some visual contact. Inside brackets the total number is given, including encounters in which the animals were heard but not seen.

Seasonality is also reflected in the frequency with which some primate species were encountered (see Table I.6). This is probably due to changes is the activity level in some species (see also section I.4.1). The effort in looking for primates was similar during all the study period - see table I.11 in section I.3.

I.2.6 - Sympatric animals

BIRDS

Willis (1979) listed 202 bird species for B.R. forests; he compared the diversity at B.R. with the diversity in two other (smaller) woodplots on São Paulo tablelands. He believed that the lower diversity found in the smaller plots was due to loss of species after forest size reduction. The first species to be lost were those of large frugivores and large insectivores. At B.R. such "sensitive" categories are present and sharing resources with a diversified primate fauna which the other two woodplots lack. It seems from this that B.R. is not an artificially impoverished environment.

There is probably some competition between birds and primates at B.R.. Potential competitors are those species which are abundant, of large size, and whose dietary category is similar to that of the Cebids; some are mentioned in Table I.7. Small but very abundant birds like Chiroxiphia caudata (understorey omnivore) and Pyriglena leucoptera (insectivore feeding on large ground arthropods) may compete with the local Callithrix, if they, like C.j.jacchus, also feed extensively on understorey arthropods..

TABLE I.7
BIRD SPECIES THAT MAY COMPETE WITH B.R. PRIMATES FOR FOOD

FAMILY	SPECIES	DIETARY CATEGORY (acc.Willis 1979) F= frugivore O= omnivore I= insectivore	ABUNDANCE (acc.Willis 1979) [n.indiv.seen in 100 field hours]
Columbidae	Columba cayennensis	F (large fruit)	42
Cracidae	Penelope superciliaris	F (large fruit)(*1)	22
Psittacidae	Pionus cayennensis	F (large fruit)(*2)	71
Ramphastid.	Ramphastos toco	F (large fruit)(*3)	35
Trogonidae	Trogon surrucura	O (large fruit/ins.)	52
Momotidae	Baryphtengus rufficapillus	I (large ground arthropods)	30
Cuculidae	Piaya cayana	I (midlevel I)	36

(*) - Species observed to eat plant items also sought by primates (1-Nectandra aff. spixiana, 2-Copaifera langsdorfii, 3-Copaifera langsdorfii and possibly Psidium sp (sample 7546))

MAMMALS

There is no systematic survey of the mammals present at B.R. forest. Local people report the presence of a series of medium to large sized mammals; I was able to confirm the presence of several of them (Tables I.8, I.9 and I.10). Small mammals have not been studied. I saw a few small-size rodents, but not bats or small marsupials. Fig.I.10 shows the places where mammals were observed.

The encounters with mammals along a well-sampled "transect" of 1200m suggested that some species were more frequently found in certain sub-habitats. For instance, Mazama and Dicotyles were more frequently observed in the part of the transect located in vegetation type B (fig.I.10), Mazama almost exclusively so. However, in the case of Mazama such apparent preference for habitat B may not be a species characteristic; I suspect that all my encounters with Mazama involved only one or two animals with a fidelity to a restricted area (perhaps a sleeping area). In the case of Dicotyles, the "preference" for vegetation B may be seasonal. Dicotyles were seen mainly during the dry season (Table I.10), and may spend most of the wet season outside the intensive study area.

The parts of the forest which are favoured by the various mammals cannot be directly identified from the scores in Fig.I.10 because some hectares were sampled more than others. To test whether a given species was preferentially found in a sub-habitat, I first calculated the expected number of encounters in each hectare (correcting for differential sampling) and then, assuming that the number of encounters in each hectare followed a Poisson distribution, I identified the hectares where the observed scores

TABLE I.8
MEDIUM TO LARGE-SIZE MAMMALS OF B.R.,
AND THE NUMBER OF TIMES THEY WERE SEEN OR HEARD DURING FIELD WORK.

ORDER	FAMILY		SPECIES	N. OBS
Marsupialia	Didelphidae		Didelphis albiventris (large American opossum)	2
Primates	Callitrichidae		Callithrix jacchus (= C.aurita) (marmoset)	44
	Cebidae		Cebus apella (capuchin monkey)	256
			Callicebus personatus (titi monkey)	117
			Alouatta fusca (howler monkey)	128
			Brachyteles arachnoides (woolly spider monkey)	41
Carnivora	Procyonidae	**	Procyon ?cancrivorus (racoon)	0
			Nasua nasua (coati)	15
	Canidae	*	Dusicyon gymnocercus (South American "fox")	0
	Felidae	*	Felis concolor (puma)	0
		**	Felis yagouaroundi (jaguaroundi)	0
		**	Felis wiedi (Margay cat)	0
		**	Felis pardalis (ocelot)	0
Rodentia	Cuniculidae	**	Cuniculus paca (paca)	1
	Sciuridae		Sciurus ingrami (tree squirrel)	17
	?Cricetidae			
	?Echimyidae			
	Dasyproctidae		Dasyprocta azarae (agouti)	79
	Erethizontidae		Coendou sp. (prehensile-tailed porcupine)	1
Edentata	Dasypodidae		Dasypus novemcinctus (nine-banded armadillo)	4
			Euphractus sexcinctus (six-banded armadillo)	1
Artiodactyla	Cervidae (***)		Mazama ?rufina (brocket deer)	1
			Mazama ?americana (brocket deer)	1
	Tayassuidae		Dicotyles tajacu (white collared peccary)	56
			Tayassu pecari (white lipped peccary)	18

* - only tracks were observed.
** - species whose presence has been reported by hunters or locals. Most of them are nocturnal.
*** - deer heard 18 times. Could be either species.

TABLE I.9

THE TIME OF YEAR WHEN SOME B.R. MAMMALS ARE THOUGHT TO PRODUCE YOUNG

The months in which young of various ages were observed is indicated by "*". The month in which their birth should have happened is indicated by "B"; because in most cases birth-time was inferred from the size and behaviour of the young, the position of "B" is only approximate.
(*) - indirect evidence ; R - rainy season; D - dry season

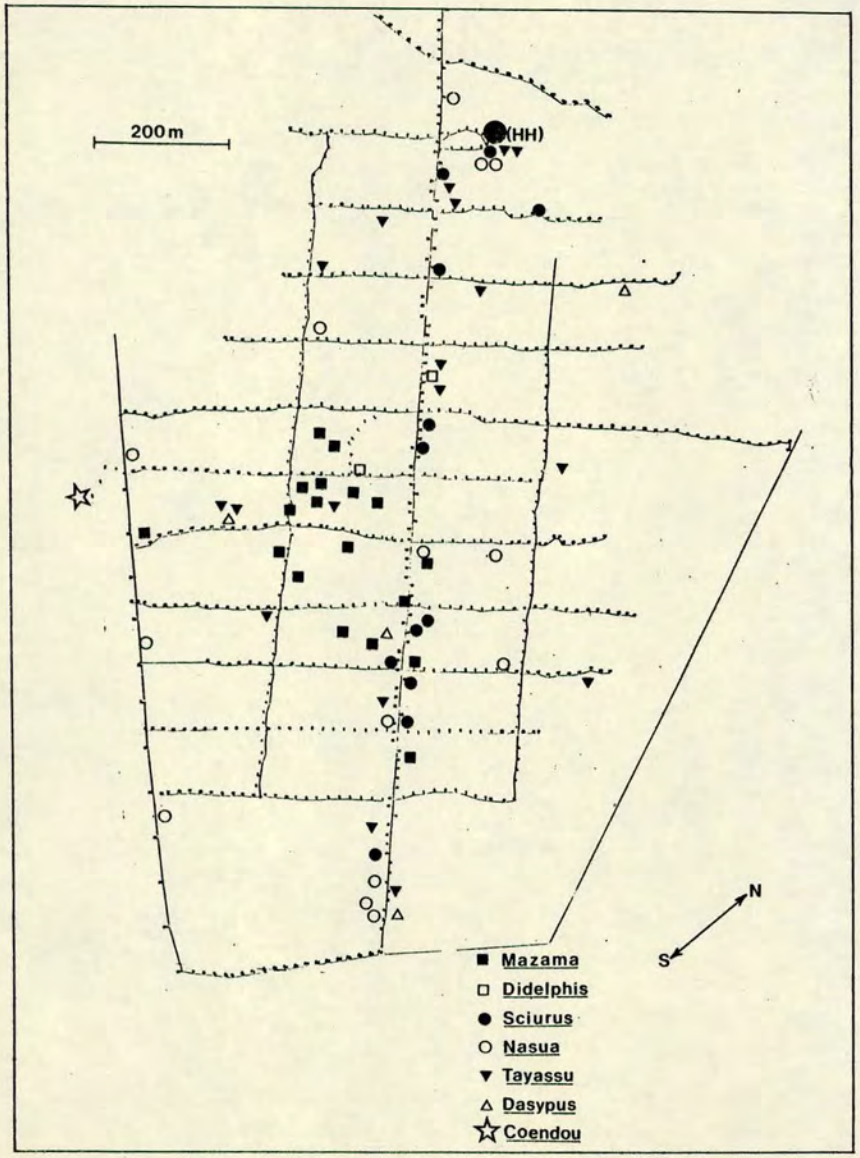
SPECIES	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Cebus apella	B	B*	B*	B*		*	*	*	*			B*
Alouatta fusca	*	*					B*	B*	*	B*	*	*
Brachyteles arachn.	B	B*		B*	*		*			B*		*
Callicebus person.		*								B	B*	
Callithrix jacchus				*	*		*				B	B
Dicotyles tajacu		*			*	B*						
Sciurus aestuans									(*)	B?		
Dasyprocta azarae					B	B	*					
Tayassu pecari	B*									*		B
Mazama sp												B*
Felis concolor		B(*)										
Nasua nasua	*						*				B	B*
SPECIES REPRODUCING:	3	3	1	2	1	2	1	1	0	4	4	5
SEASON:	R	R	R	D	D	D	D	D	D	R	R	R

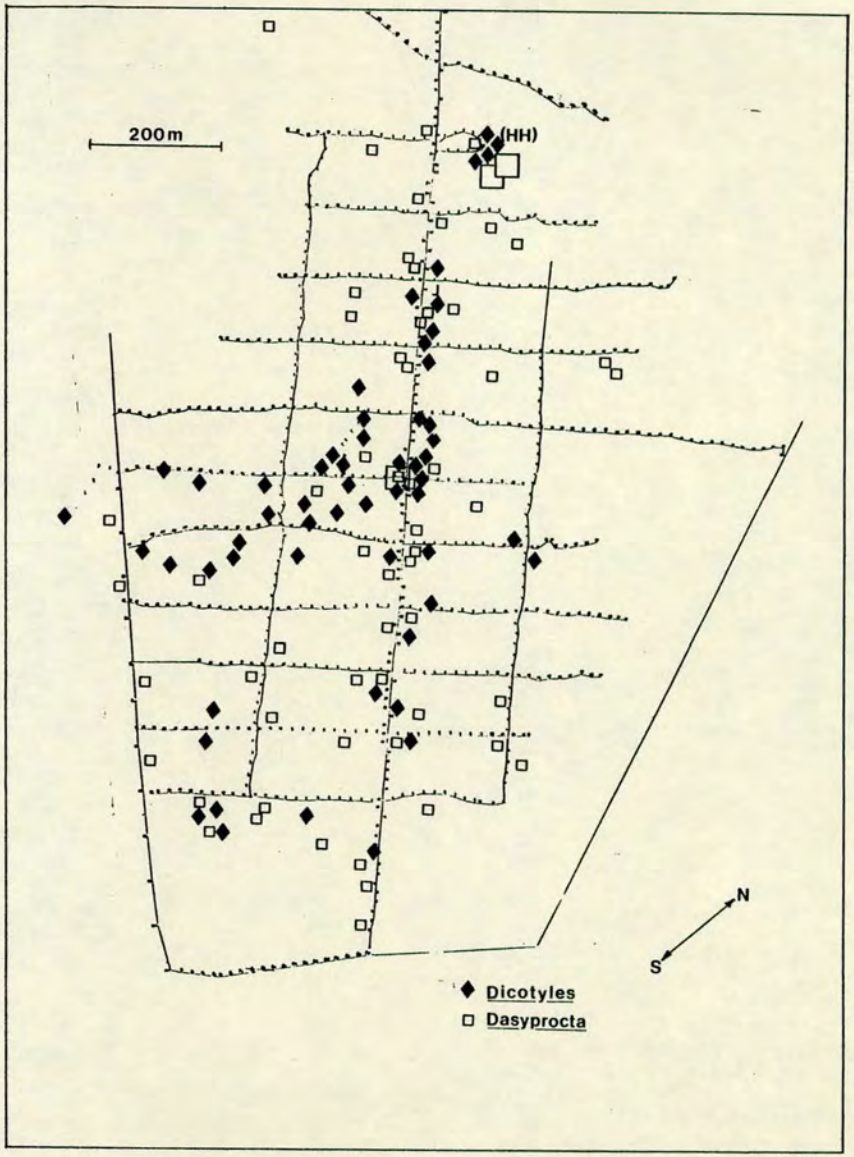
TABLE I.10
TEMPORAL AND SPATIAL DISTRIBUTION OF ENCOUNTERS WITH B.R. MAMMALS

SPECIES	FREQUENCY OF ENCOUNTERS (Dry season) IV-VI	VII-IX	(Rainy season) X-XII	I-III	N.HECTARES KNOWN TO BE USED	N. HECTARES THAT ARE USED PARTICULARLY OFTEN
Dasyprocta	9	21	37	12	40	2 (one around hunting hide; one in veg.B)
Dicotyles	17	25	7	7	30	2 (one in veg.A; one in veg.B)
Mazama	7	5	2	4	10	nil
Tayassu	4	6	3	5	14	nil
Sciurus	6	3	2	6	9	1 (hectare including hunting hide)
Nasua	0	3	4	8	11	1 (margin of forest)
Dasypus	0	2	2	0	4	Insufficient data
Didelphis	2	0	0	0	2	Insufficient data
Coendou	0	0	1	0	1	Insufficient data

Fig.I.10 - Location of encounters with mammals at the intensive study area. This is the same trail network shown in Figs. I.5 and I.7. Large symbols indicate n=5; all others n=1.

HH=hunting hide where corn was often placed to attract peccaries and agoutis.


200m
(HH)
N
S
Mazama
Didelphis
Sciurus
Nasua
Tayassu
Dasypus
Coendou


200m
(HH)
N
S
Dicotyles
Dasyprocta

had $p<0.05$. The results are summarized in Table I.10. Although there were a few hectares where the number of encounters was particularly high, this seemed to be because either that hectare included a hunting hide (Sciurus, Dasyprocta), a sleeping burrow (Dasyprocta) or a common path (Nasua). Since in none of the tested species were there several hectares in the same habitat type which were "very used" or "very little used", there does not seem to be either a very strong preference or a very strong avoidance for particular types of vegetation.

OTHER ANIMALS

REPTILES: Venomous and non venomous snakes were collected (samples housed in S.Paulo Museum) and lizards (Anolis, Tupinambis) were observed very occasionally. Reptiles can be eaten by Cebus (Baldwin & Baldwin 1977, for C.capucinus)

MOLLUSCS: not commonly observed (Megallibulimus, Helicina, Cyclodontina, Mirinaba and others). These are potential food sources for some primate species.

ARTHROPODS: Large colonies of Isoptera and Hymenoptera (ants) are common in the forest; their winged forms are a rich (but temporary) food source for several animals, including primates.
Medium size Hemiptera and Coleoptera were collected. Dung-beetles are almost invariably found in Alouatta and Brachyteles faeces, but not in the faeces of Cebus or Callicebus (this may be linked with the more folivorous diet of Brachyteles and Alouatta).

Diptera (flies, mosquitoes) are abundant throughout the year, although apparently more so during the rainy season.

Immature ticks are very abundant during the dry season.

I.3 - THE PRIMATE POPULATION AT BARREIRO RICO

I.3.1 - Methods

I.3.1.1 - Period of observation

Data were collected between January 1979 and February 1980. During 1979 an average of 9.6 days/month (range: 7-13) was spent in the forest ("day" being approximately the period from dawn to dusk). In 1980 only a few days were spent at the site. Total number of field hours: 1310.

I.3.1.2 - Area studied

Data come mainly from an intensive study area of circa 115-ha (Figs. I.3 and I.5), although occasional surveys were done in other parts of the forest.

I.3.1.3 - Trails

During the entire study period, trails were being continuously cut through the 115-ha study area (by myself and a farm worker). The timing of trail cutting caused some parts of the study area to be frequented more than others; this was taken into account during the analysis (see Appendix I.7). I mapped the trails using compass and measuring tape and at ca. 15m intervals along the trails the location was identified by a numbered plastic ribbon tied to the nearest tree. The resulting trail map (Figs.I.5 or I.7) was used to plot all the encounters with mammals.

Because I ignored the slight ground inclination when mapping the trails, the final map is 5.7% more spread than it should be

(determined by superimposing the trail map on an aerial photograph). Such mismatch is not serious for the present purposes.

When I knew a troop's whereabouts from the previous evening, I tried to find it early in the morning. Otherwise, I went around the trail system looking for primates; I used no predetermined route but tried to survey all available trails equally. When I found primates, I followed them for as long as possible, with few exceptions (e.g., I might leave them to check the identity of a nearby troop); if the animals moved into areas not accessible by trails, the pursuit was generally discontinued.

I recorded the time and location of each encounter, the number and behaviour of the individuals observed and, if possible, their identity. Notes were taken intermittently at intervals ranging from 5 to 15 minutes, as dictated by changes in the animals' behaviour and in visibility. This interval therefore varied according to the species and their behaviour at the time.

If I heard a primate vocalization, I recorded the direction from which it came, the species, the time, and an estimate of how far off the caller was. I only tried to find the caller if it was reasonably near and in an area served by trails. The distance estimate was often a subjective assessment like "very far", "near", "not far". For each species these categories correspond to different distances; this was checked on occasions when either the call was long enough to allow compass bearings from several points, or on occasions when the caller was found after vocalizing. Such distances (below) were used to plot primates that were heard but not seen.

	"NEAR"	"NOT NEAR, NOT FAR"	"FAR"
Alouatta	<100 m	around 400 m	800+ m
Brachyteles	<100 m	around 250 m	500+ m
Callithrix	< 20 m	around 50 m	100+ m
Callicebus	<100 m	300 to 400 m	600+ m
Cebus	<100 m		200+ m

I.3.1.5 - Other obervations

Notes were also taken on:

a. time and place of encounters with any mammal, the number of observed individuals and their behaviour;

b. any information on predation on animals or plants (e.g. from carcasses, faeces);

c. weather (notes on rain periods, cloudness, max./min. temperatures, relative humidity).

I.3.1.6 - Time of observations

The absolute time of the observations was ignored; all were ascribed to a given "day phase", to compensate for the different day lengths at different seasons. Sunset and sunrise times for B.R. were obtained by adding six minutes to the times reported for São Paulo city in the ANUÁRIO ASTRONÔMICO (1975). This addition compensates for the difference in longitude between S.Paulo and B.R. (I.Varella, pers.commun.). The difference in latitude is negligible for the present purposes. For each month an average sunrise and sunset time was calculated, and the light period of each day was divided into ten "day phases" of equal duration. The number of day phases I spent in the forest varied only very slightly between months (see Table I.11); it can be said that the primates had equal chance of being observed in all day phases.

TABLE I.11
NUMBER OF DAY-PHASES SPENT IN THE FOREST DURING 1979

MONTHS	DAY PHASES I	II	III	IV	V	VI	VII	VIII	IX	X
Jan. to Mar.	24	24	25	26	25	25	25	24.5	24	23
Apr. to Jun.	26	26	25	25	25	26	27	27	27	27
Jul. to Sep.	26	26	26.5	27.5	28	26.5	26	26	27	27
Oct. to Dec.	22.5	24.5	25.5	26.5	26.5	26.5	26.5	27	28	23

I.3.2 - RESULTS

I.3.2.1 - Differences in the primates' conspicuousness

The amount and type of information obtained varied widely between species, as shown by the following breakdown:

For a stay of 1310 hours in the field,

	HOURS OBS.	% TOTAL TIME SPENT OBSERVING PRIMATES	N. OF ENCOUNTERS (at least some visual contact)
CEBUS	284 h 33	77.9	256
ALOUATTA	41 h 00	11.2	41
BRACHYTELES	23 h 22	6.4	31
CALLITHRIX	12 h 29	3.5	40
CALLICEBUS	3 h 33	1.0	15
	364 h 57	100.0	383

The above is equivalent to:

	AVERAGE INTERVAL BETWEEN ENCOUNTERS (hours)	AVERAGE DURATION OF ENCOUNTER (minutes)
CEBUS	5	66
ALOUATTA	32	60
BRACHYTELES	42	42
CALLITHRIX	33	19
CALLICEBUS	87	14

The reason for the discrepancies above were the peculiarities of each species:

Callicebus were difficult to find and follow because they move without noise and hide from observers. They often vocalize in the morning, but if not spotted at that moment, they cannot be found easily, even if their general whereabouts is known. If one keeps

staring at the exact spot where they hid, after around 20 minutes they will peer down and emit soft distress calls. They then move quietly to another spot, and hide again.

Callithrix could only be located from relatively short distances (around 200 m). They were generally located through their vocalizations (the whistle-twitter or the softer 'tss-ka' emitted at an observer's approach). Their preference for very entangled understorey makes them difficult to follow, but they may approach stationary observers to within 5m.

Brachyteles could be spotted through the noise they produce when moving, or through their vocalizations. Once spotted, these animals are relatively easy to follow and observe. Although obviously aware of observers, Brachyteles often ignore them. As Brachyteles seemed to prefer parts of the forest not served by trails until the last weeks of the study, most data on this species was collected on the few occasions when they entered more accessible areas.

Alouatta could be located through their roaring calls, but often I spotted them when they were silent. Alouatta are slow-moving, but to keep contact is not always easy. However, the mean encounter time quoted above is less than it could have been, since on some occasions I left resting howlers to look for other animals. Because of their tendency to remain immobile, it takes hours to obtain a reliable group count. As in the case of Brachyteles, these primates may ignore observers.

Cebus was more often encountered than any other species. This is only in part because of their abundance. They are also more noticeable than the other species, due to their:

a) noisiness (vocalizations and branch movement),

b) wide group spread (often more than one hectare),

c) ability to cross large distances relatively fast and

d) high level of activity.

Although it was relatively easy to keep in touch with part of the troop, individual animals were rarely in sight for more than a few seconds. As a rule I was unable to follow individuals to sample from, and had to observe the most conspicuous or boldest animals. The Cebus at B.R. were persecuted in the past, and this made them very wary. They invariably avoided being observed, and showed no sign of habituation during the study period. Cebus were more affected by hunting than the other local primates because they are the only local primates that descend to the ground to eat bait corn at hunting hides. The bait is actually intended to attract peccaries, but hunters may fire at the Cebus' tails to punish them for stealing the bait.

I.3.2.2 - Distribution of primate groups in the intensive study area

In this study I did not estimate the primate population through transect sampling, but by censusing the population of a restricted area (the intensive study area). A model was then produced for each species to accommodate all the information obtained for that species. As most primates associate in groups, an important aspect of the modelling was the use of all indications

that there were independent groups in the intensive study area. The term group here refers to isolated sets of individuals of a given species. Groups are expected to be natural social units, but might not be. The term troop will be used here only to refer to what I believe are real social units. It is assumed that during the study period the relationship between troops remained constant.

Indications of independence between groups include:

(a) vocalizations from different locations, heard simultaneously or almost simultaneously (commonly the case in Callicebus);

(b) sightings of groups at different places within too short a period to allow the same group to have moved from one to the other (commonly the case in Alouatta);

(c) simultaneous sightings by different observers at different places;

(d) recent tracks or faeces (very rarely used)

There is some decision-making involved in the acceptance of group independence (particularly in the case of (b) above, since a group's spread and travelling speed may vary). To minimize errors I used only the safest indications of group independence. These are generally reliable if the group members stay near each other (as is generally the case for Alouatta and Callicebus), but less so in the cases where the social unit spreads over a large area (Cebus), or splits temporarily.

For each set of consecutive days spent in the forest, I plotted all the available information on the primates' location; then, taking into account the time and location of encounters/vocalizations, and also the travelling speed of each species, I looked for indications of independence between groups.

Table I.12 shows the NUMBER OF INDEPENDENT GROUPS detected in each set of days. The figures in Table I.12 do not directly indicate the total number of groups in the intensive study site, because each set of days is likely to provide information on just part of the population. To obtain a global picture, the information about the number of independent groups was integrated with other types of information, such as the PLACE where the simultaneous encounters or vocalizations happened, the observed TROOP SIZE AND COMPOSITION, or the sighting of KNOWN INDIVIDUALS. Because for each species the amount of each type of information varied, so did the method used to build the models. In the case of species where each social unit occupies a geographically fixed area, a model can be built by simply integrating the information about group independence and group location. This method is described in Appendix I.4. The method is very reliable for territorial species where the home range coincides with the territory, less so for species with defended core areas but with some overlap of home ranges and unsuitable for species where the troops have extensive home range overlap. Because it assumes that troops are geographically fixed, the method is not suitable for nomadic species and can only be used for species which have spatiotemporal territories if the study period is short. I used this method for Callicebus and Callithrix. For Alouatta the method was tried and produced several reversals (see Appendix I.4), indicating that it is not very appropriate. The population of Alouatta was estimated by a variation of this method. For Cebus the method could not even be tried because field observations had indicated that there was much overlap between the home ranges of different groups, and so Cebus population was estimated through the

TABLE I.12

NUMBER OF INDEPENDENT GROUPS OF THE SAME SPECIES DETECTED IN EACH SET OF CONSECUTIVE DAYS SPENT IN THE FOREST

SET N.	N.of consec. days	Data sheet (*)	SPECIES				
			BRACHY.	ALOUAT.	CEBUS	CALLIT.	CALLIC.
1	3	1	-	-	-	-	2
2	3	2	-	-	2(2)	-	2
3	3	3	-	(2)	-	-	3;2
4	3	4	-	2;3	-	-	3
5	4	5	-	2	(2)	2	3 (or 4)
6	2	6	(o)	-	2	-	-
7	3	7 & 8	-	4	2	-	2;3
8	3	9 & 10	-	2	(2)	-	-
9	2	11 & 12	-	(2)	(2)	2	3(or4);2
10	8	13 to 18	-	2;2(or5)	3;2(or3); 2;(2;2;2)	2	2;2;2
11	4+1	19	-	2,2	3;2(or3)	3	3 (or 4)
12	4	20	-	3;(2)	2;2	-	2;2
13	5	21	-	3	2	-	3
14	4	22	-	3	(2);(3)	-	-
15	5	23	-	2;3;2	2	-	2
16	5	24	-	2 (or 3)	(2);(2)	-	3
17	6+1	25	(o)	2;3	(2);2	-	5;3;2;2
18	2	26	-	2	(2)	-	3 (or 4)
19	6	27	-	(2);2	(2);(3)	-	3
20	2	28	-	2	2	-	3 (or 4)
21	3	29	-	2 (or 3)	(3)	-	-
22	4	30	-	(2)	2	-	2
23	2	31	-	2	(2)	2	4
24	4+1	32	-	2	(2)	-	-
25	4	33	-	2;3	-	-	2
26	4	34	-	3;3	-	-	2
27	3	35	-	-	(2)	-	-
28	3	36	-	3	(2)	-	2
29	2	37	-	3	(2)	-	-
30	2+1	38 & 39	-	2	-	-	-
31	2+1	40	-	2	-	-	2;2

* - quoted since the numbers quoted in Fig.I.13 and I.16 are the original data sheet numbers, not the set of consecutive days.

() - possible number of independent groups

(o)- one group in the intensive study area and another more than 1km away

Empty cells in the table above do not mean that the species was not seen or heard, only that independence between groups was not detected.

integration of two types of information: the location of recognized individuals and the indications of group independence. For Brachyteles there was no indication that there was more than one group in the intensive study area, so there was no need for modelling. The results obtained, and also their reliability, are discussed separately for each species, in sections I.3.3 to I.3.7.

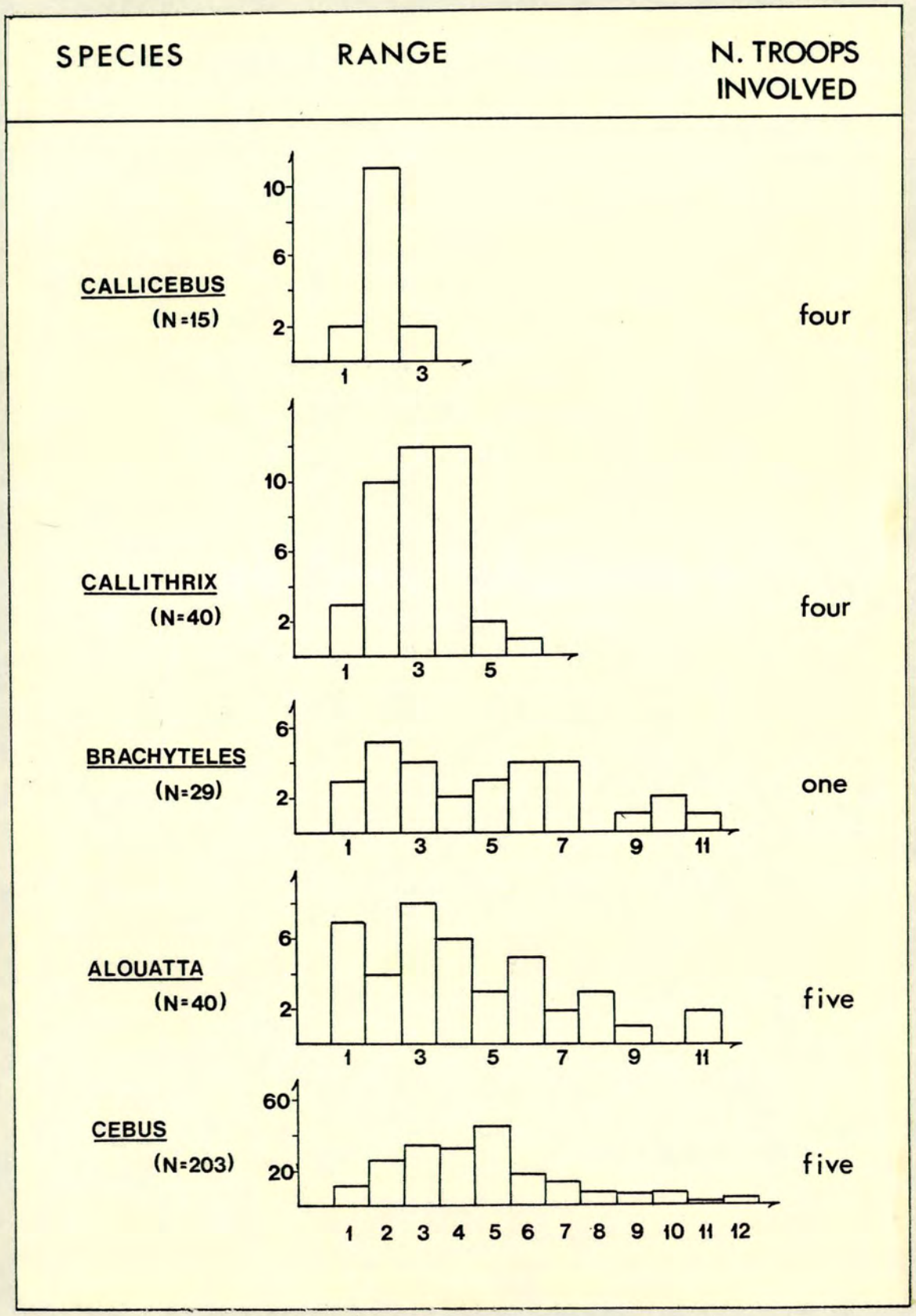
I.3.2.3 - Composition of troops

Callicebus and Callithrix adults are not sexually dimorphic and for these species I was generally unable to distinguish the sexes. The adults of Cebus, Brachyteles and Alouatta can be more easily sexed, due to their sexual dimorphism in size (and also in colour, in the case of Alouatta). Distinction of age classes was done on the basis of relative body size. In the case of Cebus age classes could also be distinguished by the cap shape and the size of its tuft (see Fig. II.5)

I.3.2.4 - Troop counts

The reliability of troop counts varied between species. Fig.I.11 shows the observed troop sizes. In many cases the counts include both animals seen and animals only heard; when counts are based only on animals SEEN, dependent infants are not counted. This makes the counts more consistent, as dependent infants should not be HEARD as independently locomoting individuals in other encounters. For Brachyteles all encounters seemed to involve the same troop, so the troop size is probably the largest number of observed animals. For the other species the counts involved several troops, so differences

Fig.I.11 - Number of individuals observed in the various encounters with primates. X-axis: number of individuals; Y-axis: number of encounters



in the counts are not only due to observational difficulties and to temporary splitting of the troop, but also to real differences in size between troops.

I.3.3 - *BRACHYTELES ARACHNOIDES*

NUMBER OF TROOPS

Although one cannot be completely sure without marking the individuals, it seems, from the location of encounters, group composition and age of infants, that all encounters with *Brachyteles* in the intensive study area involved only one troop.

AREA OCCUPIED

The troop mentioned above was seen to enter 60 one-hectare quadrats; this is only a fraction of its home range, as indicated by the lack of a plateau in the cumulative home range graph for the study period. There are at least 45 other quadrats of the intensive study area that may be in principle ascribed to the same troop, since their location (isolation by roads) makes them inaccessible to other *Brachyteles*, and they are a natural extension of the troop's observed range (see Fig. I.12). Thus, at least 105 hectares are available for a troop of around 13 *Brachyteles* (11 independently locomoting animals plus 2 infants).

TROOP SIZE AND COMPOSITION

The best counts for the *Brachyteles* troop in the intensive study site indicated the following composition:

4 males (all of adult size with large pendulous scrota)

4 females (including at least 3 of breeding age)

2 juveniles (1 male and 1 female)

1 independently locomoting infant (sex unknown)

2 dependent infants

Smaller counts (Fig.I.11) were due to the splitting of the troop during the day. Groups of 30+ individuals have been observed at B.R. (L.Magalhães, pers. com.), but outside the intensive study area. Groups of this size may be seasonal associations of the type described for Lagothrix (Durham 1975, p.97), but they could also be the product of short encounters between neighbouring troops. Such encounters may be frequent; on the two occasions when I had information about the distance between supposedly neighbouring troops they were ca. 2,500 m apart, and Brachyteles may cross 750m in one hour.

DENSITY

Assuming that no more than one troop uses a given area, as seemed to be the case in the intensive study area, and that in all parts of the forest the home range size is similar, the available information indicates a density of less than 13 Brachyteles/km^2 at B.R. How much less depends on how much larger than 105ha is the average home range. My estimate, based on the distance at which different troops were observed, is that the home range is around 100ha larger. This would yield a density of ca. 6 animals / km^2. The only information published on the subject is that in Aguirre (1971) for remnant forests of 170, 217 and 580ha, where densities seemed to be, respectively, 4.7, 5.5 and 5.2 animals/km^2. The apparent agreement

among figures should be taken with caution. None of these figures emerged from detailed data, but are gross estimates based on the total area available for troops of known sizes. Even if these overall densities prove correct, animals may in fact be concentrated in parts of the forest, leaving big gaps between troops.

RELIABILITY OF THE RESULTS

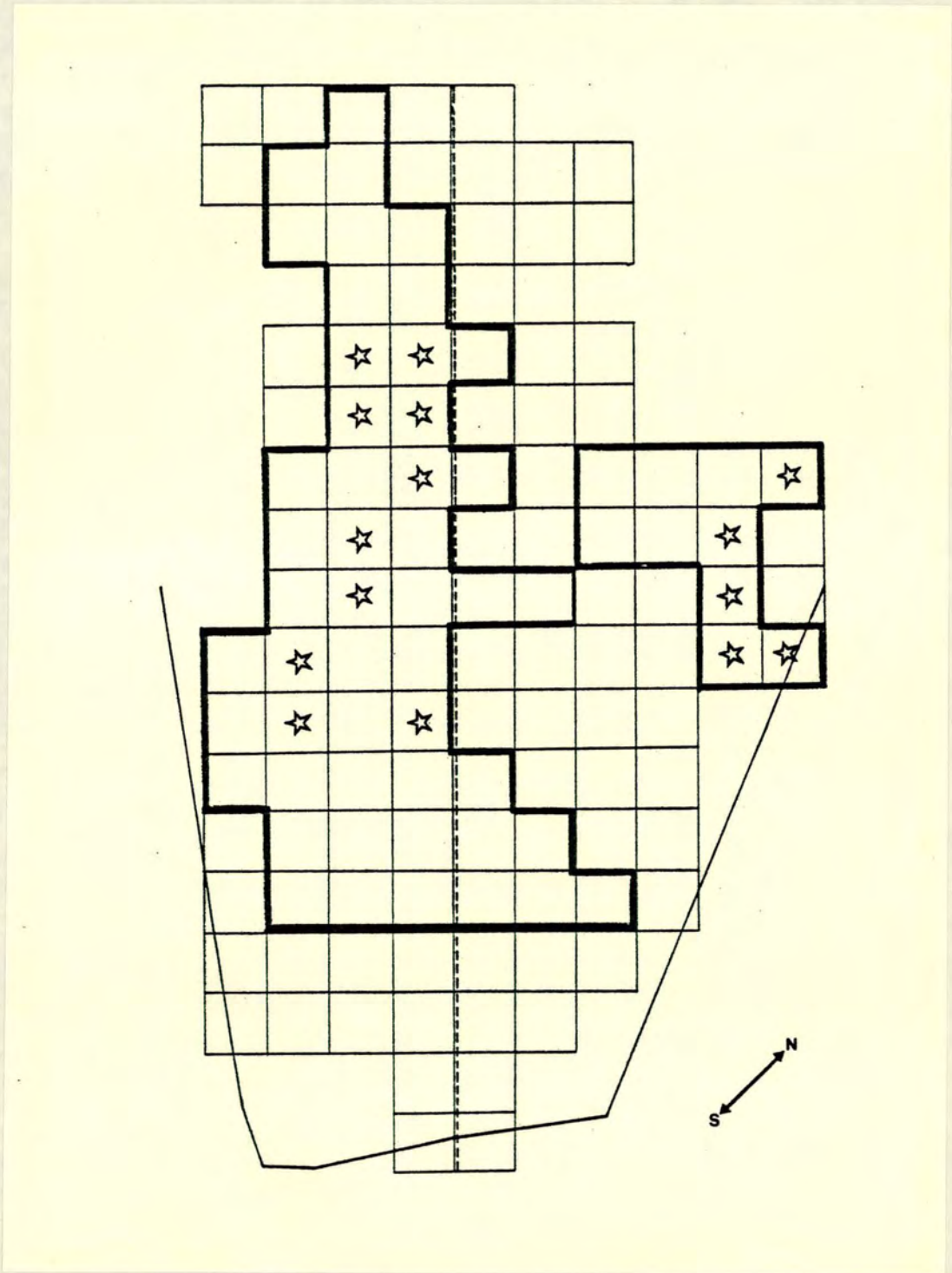
The estimates for density and home range size presented above assumed that no other troop of Brachyteles entered the intensive study area, since there was no indication of this. If I failed to observe other groups, or if what I believed to be the same troop was in fact another one with similar composition, the density indicated is an underestimate and the home range size an overestimate (i.e., assuming that troops use exclusive areas). In order to check this it would be necessary to mark animals or to place other observers at different parts of the forest.

USE OF HOME RANGE

Parts of the observed home range were frequented more by the troop than others (see Fig.I.12). The method used to determine this is similar to that described in section I.2.6 for the distribution of mammals, with the difference that, instead of the scores being the number of encounters, they were the number of 16-minute intervals during which at least one Brachyteles was seen in each quadrat. The interval was fixed at 16 minutes because, on average, this was how long a Brachyteles took to cross a quadrat.

Some of these favourite quadrats are located in vegetation type "B", but most are in vegetation type "A" (the actual scores are shown in

Fig.I.12 - The intensive study area divided into one-hectare quadrats. Those quadrats where Brachyteles were observed are outlined with thick lines. Stars indicate the quadrats where the number of scores (definition in the text) was very high ($p<0.05$).



Appendix I.7). As Fig.I.12 is based on a pool of data from the whole study period, it does not indicate how the home range use changed with the seasons. A more detailed study would probably indicate that the animals preferred vegetation type "A" during most of the year.

NOTES ON BEHAVIOUR

Brachyteles seem to alternate periods of very rapid travel with periods of virtual immobility. While travelling the animals move generally in unison. Feeding seems to occur mostly when the group is not travelling; at this time the group splits up.

The behaviour of Brachyteles will not be considered further. Some information on the distribution of Brachyteles' behaviour across the day and on their vocalizations is available in Torres de Assumpção (in press).

I.3.4 - CALLICEBUS PERSONATUS

NUMBER OF TROOPS

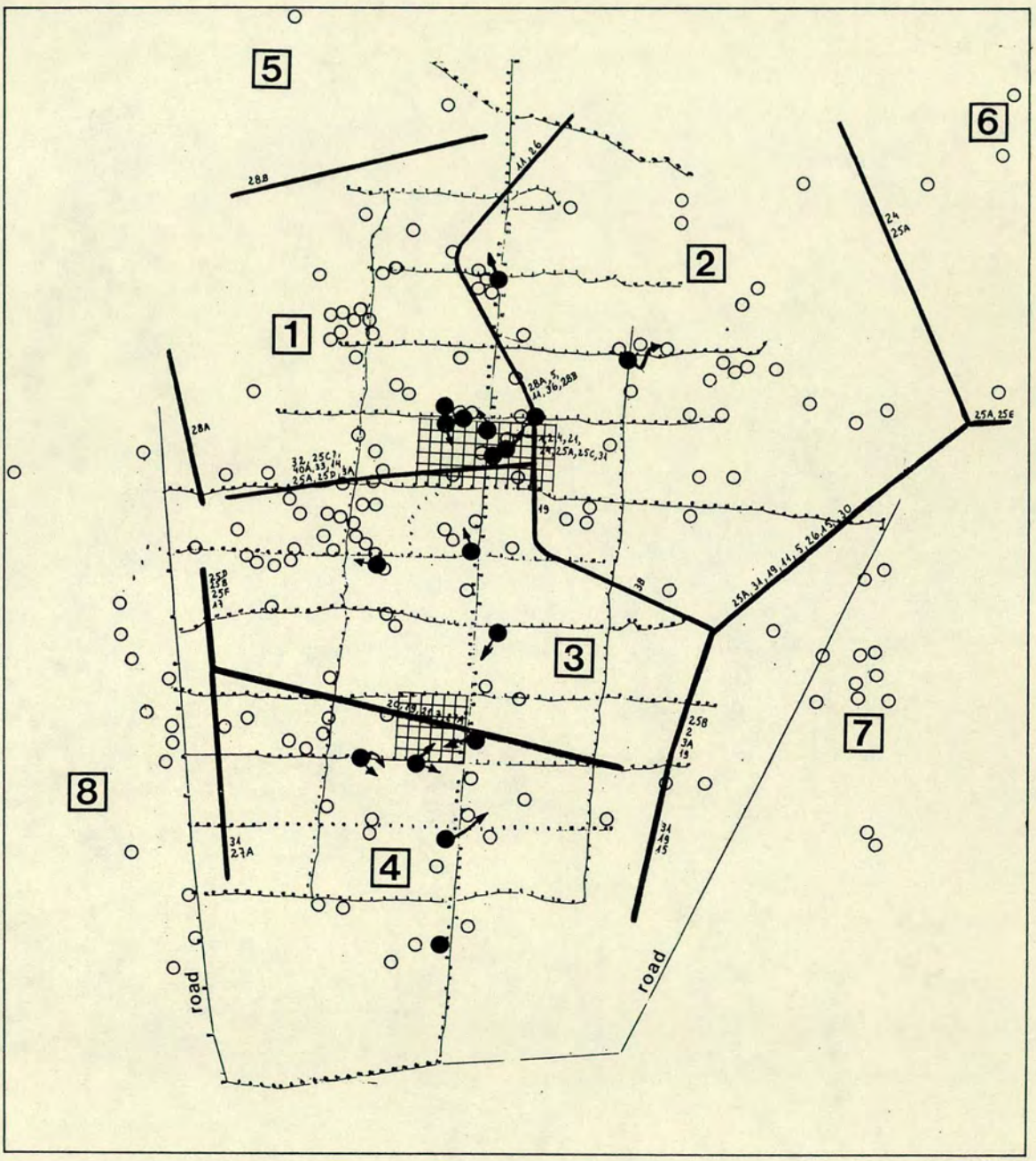
The procedure described in Appendix I.4 was applied to the Callicebus data; the resulting pattern is shown in Fig. I.13. In this figure the thick lines divide the intensive study area into four blocks (numbered 1 to 4), each thought to contain one group of Callicebus. The existence of groups outside the intensive study area (blocks 5 to 8) could be established because Callicebus calls may carry over more than 600m and were heard from the study area.

Fig.I.13 - The spatial distribution of Callicebus groups (1 to 8) in and around the intensive study area, as given by the method in Appendix I.4. The trail network is the same as in Figs.I.5 and I.7.

Each thick line was drawn based on a number of cases indicating the existence of independent groups on each side of the line. The cases are identified by code numbers written near each thick line.

Empty circles indicate the approximate location of vocalizing Callicebus (pool of data from the whole study period). The uncertainty of these points varies from zero to ± 100m.

Black dots indicate the places where Callicebus were actually seen. The arrows indicate the direction of the animals' movement. Shaded quadrats are more frequented than expected (see text on "Use of home range").


5
6
2
1
3
7
8
4
road
road

TROOP SIZE AND COMPOSITION

Although I was unable to sex the individuals observed, it seems safe to assume that the troops were family units, as in all studies of Callicebus elsewhere. Fig.I.11 shows that Callicebus were generally seen in twos, probably heterosexual adult pairs, since if three animals were seen, one was a young animal.

AREA OCCUPIED

Although, as explained in App.I.4, the dividing lines shown in Fig.I.13 are not real boundaries, they give an indication of the maximal area available for each troop, if there is (as assumed) no overlap. The following estimates were obtained for the troops of the intensive study area: 21, 31, 23 and 38 hectares (average: 28). There is no published information about the home range size of C.personatus elsewhere, apart from a suggestion by Kinzey and Becker (in press) that a troop of six Callicebus personatus in Sooretama (State of Espirito Santo, Brazil) used at least 11.5ha. There is some information about the home range size for the other two species of Callicebus. C.moloch's home ranges vary between 0.5 and 6ha, averaging 4.0ha (results from several studies, quoted by Kinzey 1981). For C.torquatus there is less information; one troop studied by Kinzey over several years used up to 29ha. A less prolonged study by Robinson (pers.comm. to Kinzey 1981) indicated that C.torquatus may also occupy much smaller home ranges, of 3 to 4ha. Kinzey (1981) suggested that the differences in home range size are species determined in Callicebus; this is not necessarily the case. The few troops of C.torquatus that have been carefully examined lived in an impoverished habitat, where primates are expected to

have relatively large home ranges. C.torquatus may occupy different types of forest in areas where they are not sympatric with C.moloch, and in that case they might require less area. Since so little is known about the variation of home range size within each species, it is difficult to assess the results obtained for the C.personatus at B.R.; if they make use of all the area thought to be available for each group, their home ranges are much larger than any of C.moloch, but similar to the home range size observed by Kinzey for C.torquatus (29ha). Home range size may be species-dependent in Callicebus, as Kinzey suggested, but it may also be a mere reflection of different ecological pressures at different sites.

DENSITY

Accepting two individuals as the average group size for C.personatus at B.R., Fig.I.13 would indicate a density of 7 Callicebus /km^2. If an average of three animals per group is accepted, the density would be 10 Callicebus/km^2. Table I.13 provides comparative data for the three species.

The figures in Table I.13 are widely different, and they cannot be easily compared because they were obtained with different methods (either map census, transect census, or following of known troops). Even excluding the values obtained through transect census, it seems that Callicebus density at B.R. is low, partially because the groups are small. Whether this is typical for the species will only be known when more information becomes available.

RELIABILITY OF RESULTS

The reliability of the results above depends on whether the

TABLE I.13

CALLICEBUS DENSITY AT VARIOUS SITES

(results from several studies quoted by Kinzey 1981)

SPECIES	AVERAGE GROUP SIZE (N.INDIV. PER GROUP)	DENSITIES AT DIFFERENT SITES (N.INDIV. PER SQ.KM)
C.moloch	3.0	400+
		24
		2.1 *
		9.6 *
		13.5 *
		2.7 *
C.torquatus	3.5	0.7 *
		13.3 *
		16
C.personatus	Kinzey & Becker followed a group of 6 individuals	No information available

(*) - based on transect census, and suspected by Kinzey (1981) to be underestimates.

assumptions mentioned in App.I.4 are acceptable. The first assumption is that each group remained fixed to a given area during the study period. This is probably true for the study period, but it may not be so for a longer period, as observed by Kinzey and Robinson (1981) for C.torquatus. C.personatus seems similar to C.torquatus in the use of large home-ranges and in the use of their calls to space groups (see section on behaviour). If boundaries are not defended, and troops simply keep themselves spaced out, the boundaries may not be well defined and this could result in their gradual shift. This may be happening at B.R., but because the study period was relatively short, it is unlikely that shifts, if they happened, would have been very drastic. Also, the dividing lines are coarse and not necessarily the real boundaries. The method allows for these lines to coincide with the boundaries as data accumulates, but at this stage they are insensitive to minor shifts of boundaries. So, as far as the first assumption is concerned, the results presented can be considered as an acceptable estimate.

The second assumption is that the study was long and intensive enough to allow collection of information on the independence between all groups present in the area. Because of the contagiousness of the calls, it is reasonable to assume that all troops would have responded to calls at one time or another, and thus had a chance of having their independence recorded.

The weakest aspect of the method is the decision about whether two vocalizing animals belonged to the same troop or not. Although members of the same troop are rarely far apart (see Fig.I.14A and also Fragaszy & Mason (1978)), they might occasionally separate and call while apart. If I heard animals calling within 100m of each

other, and could not observe their behaviour, I assumed that they were members of the same troop, but this might not necessarily be so. However, this problem did not often arise, as in most cases the calls came from points far apart, i.e., almost surely from different troops.

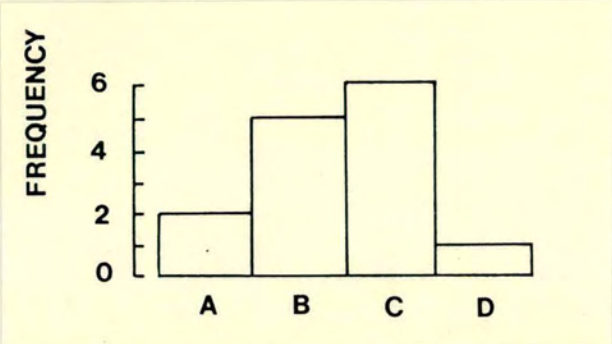
USE OF THE HOME RANGE

To investigate use of the home range, I used the same method described previously for the encounters with mammals (section I.2.6). The number of encounters in each quadrat was compared with the number of encounters expected if this variable followed a Poisson distribution. In three of the quadrats the scores were so high as to be associated with $p<0.05$. They correspond to areas that should belong to two different troops. It is not certain that they are on the home range boundaries. In both cases the area seems to be in a transition from vegetation B to vegetation A.

NOTES ON BEHAVIOUR

It was difficult to find and follow Callicebus at B.R. I only saw them on a few occasions, in 11 of which I was able to observe their behaviour before they saw me. On six of these occasions (54%) they were immobile (on two of these occasions their inactivity could have been due to the falling rain); on one occasion (9%) they were eating and on the remaining four they were moving (not necessarily travelling). Kinzey & Becker observed that this species rested in most time samples (56%) at Sooretama; "resting" was the most frequently scored behaviour, followed by feeding (18% of the time samples), followed by travelling (13%). Although my sample is very

Fig.14 A - Distance between the members of a Callicebus group when first spotted (pool of data from the whole study period)



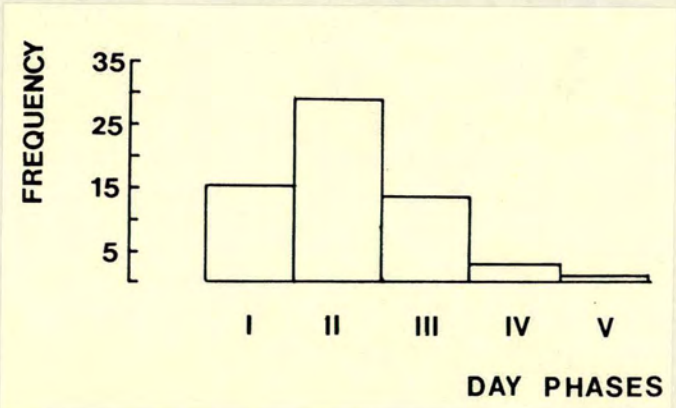
A - touching each other

B - less than 5m apart

C - less than 50m apart

D - more than 50m apart

Fig.I.14 B - Time of first Callicebus calls (pool of data from the whole study period).



Obs. - at least during winter I was in the forest well before dawn.

small, it matches the results obtained by Kinzey & Becker and suggests that at B.R. Callicebus also rest a lot.

I did not observe Callicebus jumping large gaps between trees, and they often hesitate before changing branches. They seem to move carefully and slowly, and probably take a long time to cross areas of broken canopy. Fragaszy (1980), working with captive Callicebus, found that they do not use novel paths as shortcuts to minimize travel distance, preferring to use a longer but familiar path. It is unlikely that these animals efficiently patrol all parts of their home range, if they indeed have home ranges of the order I estimated. Their vocalizations, which are their most prominent feature, are probably very important in helping them to keep hold of an area. The importance of the vocalizations in the spacing is also suggested by its loudness and contagiousness. The exact mechanism is not known. Both C.moloch and C.personatus are said to occupy exclusive territories whose use is regulated by vocalizations, but Kinzey & Robinson (1981), on the basis of play-back experiments, concluded that the calls are serving different roles in these two species. If a playback source was placed at distances up to 100m, C.moloch would approach it, calling. On the other hand, C.torquatus ran away from the speakers placed within 50m, and only remained and called back if the speaker was 75m away. C.torquatus never approached the playback source. Kinzey & Robinson concluded that in C.moloch the calls are used to are used to maintain the boundaries, whereas in C.torquatus the call keeps troops spaced. It is perhaps not surprising that over a period of six years a troop of C.torquatus had shifted its territory's boundaries to the extent that the area occupied, although of the same size, had a totally

different location (Kinzey & Robinson 1981). The C.moloch troops that have been studied maintained their territory boundaries unchanged for at least three years. It seems likely that the C.personatus at B.R. use their vocalizations in a way similar to that described for C.torquatus, i.e., to keep groups evenly spaced. In both cases the area available to each group is large, and these slow moving animals would probably be unable to defend its boundaries. If the calls are used for spacing, animals are more likely to react to calls given nearby than to calls given far away. This seems to be the case at B.R., although the picture was not always clear. On a few occasions I observed a "chain reaction" of calls, with a group's call eliciting that of a (supposedly) neighbouring troop, which in turn elicited that of another troop further away and so on, involving up to five groups. A very similar situation has been described for Cercocebus galeritus (Quris 1980), but that author interpreted the data as being a tendency of the animals to stay within calling distance of other groups (and not calling only if too near).

C.personatus at B.R. may remain stationary and mute while hearing another troop's call, but may also move some tens of meters towards it, calling back. However, this approach covered only a fraction of the real distance between the groups.

Calls are not emitted with equal frequency across the intensive study area. I considered the 400m-wide strip on either side of the main trail (therefore the best sampled area) and compared the number of calls emitted from each quadrat of ~16ha using a chi-square test. Homogeneous distribution of calls was rejected at $p<0.01$ (d.f.=7, $\chi^2=79$). It was necessary to use large

quadrats because of the uncertainty in plotting the precise location of the calls, and also because the chi-square test requires that the expected values be at least 5 in more than 20% of the cells. These differences could be due to some groups being more vocal than others, or to some areas needing more defending than others.

An interesting aspect of Callicebus vocalizations is the time of the day when they are first emitted. Kinzey & Becker (in press) suggest that there are consistent differences between species, with C.moloch calling before dawn, C.torquatus either before dawn or at dawn, and C.personatus after dawn. At B.R. the first Callicebus calls are produced well after dawn, mainly during day phase II, as shown in Fig.I.14B.

In spite of the calls being more frequent in a certain day phase, which implies some relationship with dawn time, the correlation between the average dawn time and the average calling time in each month is a weak one ($r=0.50$, $n=12$). This indicates that other factors are influencing the time of calls. A possible one is weather. At B.R. there seemed to be a tendency for Callicebus to call when the weather changed from overcast to clear (although calls may be heard under any weather condition, including rain). Kinzey (pers.comm.) noted the same tendency in the Callicebus at other sites. Loud calls are expected to be given at the time of the day when the atmospheric turbulence produces less fluctuation in the range of sound propagation (Quine 1981). Calls would then be expected at different times on different days depending on the weather. Calling time would also vary between sites.

Calls may be emitted at any time during the day, and occasionally after sunset, but most calls after day phase V seem to

be motivated by troop disturbance (e.g. caused by Cebus approach) rather than by intraspecific spacing. Nevertheless, a call produced by a group that has been disturbed by Cebus may elicit vocalizations from other Callicebus groups.

I.3.5 - CALLITHRIX JACCHUS (= C.AURITA)

NUMBER OF TROOPS

The procedure described in Appendix I.4, when applied to the Callithrix data, produced the pattern shown in Fig.I.15, indicating that there were four Callithrix groups in the intensive study area.

TROOP SIZE AND COMPOSITION

Fig.I.11 shows that marmosets were most frequently observed in groups of 3 or 4 individuals, but the number observed in any encounter is unreliable and cannot be used to identify groups. For example, in the area attributable to troop 4, the number of individuals observed on different occasions varied from 2 to 6. Fluctuation in group size may have been affected by the birth of individuals and some animals avoiding being observed. I suspect that individuals carrying infants, and also young independent infants would do the latter because, although infants must have been born during the period of field work, I did not observe any dependent ones, and only saw independent young animals very occasionally after April.

The largest count in each of the four areas of Fig.I.15 were: 4, 4, 3 and 6 (respectively troops 1 to 4). There is no information in

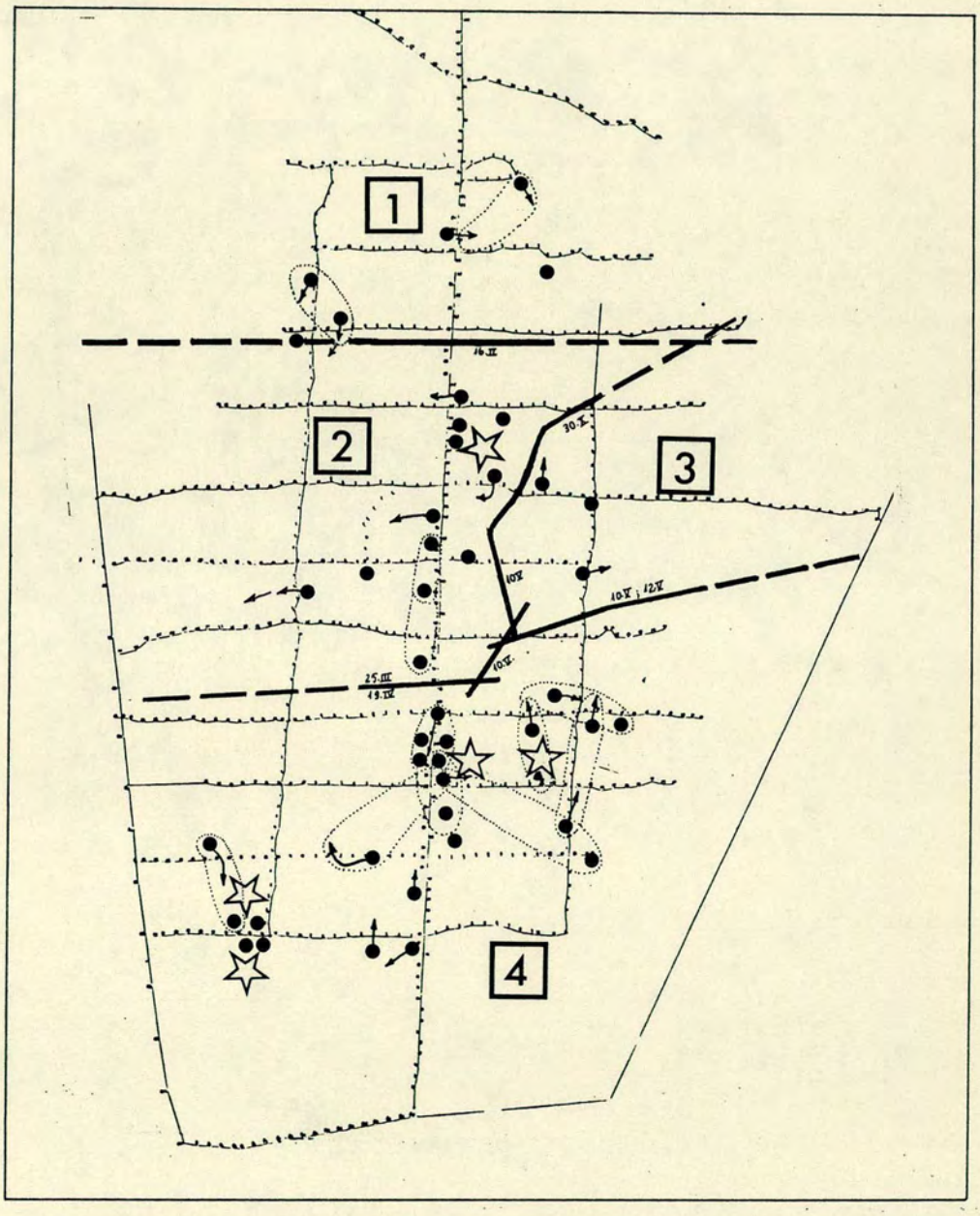
Fig.I.15 - The spatial distribution of Callithrix groups (1 to 4) in the intensive study area, as given by the method described in Appendix I.4. The trail network is the same as in Figs.I.5 and I.7.

Each thick line was drawn based on a number of cases indicating independent groups on each side of the line. The cases are identified by the dates written near each thick line.

Black dots show the places where Callithrix were actually seen, with arrows showing the direction of their movement.

The one-hectare quadrats where the number of encounters was significantly higher than expected are marked with stars.

The thin dotted lines indicate areas believed to be parts of the home range of the same troop (indicated, for instance, by two encounters in the same day); the picture they produce is consistent with the thick dividing lines.


1
2
3
4

the literature about group size in C.jacchus aurita, but for the other races the figures are all very similar. The C.j.penicillata observed by Fonseca et al. (1980) lived in groups of 2 to 8 animals, generally 5 to 6, and the C.j.jacchus observed by Maier et al. (1982) lived in groups of 3 to 7 animals.

With the occasional exception of adult males (which have white genitalia) it was generally impossible to determine the animals' sex. C.jacchus are known to live in family units containing only one breeding pair and their offspring. Although I was not able to obtain information on troop composition of C.j.aurita at B.R., I expect that they also live in family units, like other C.jacchus.

AREA OCCUPIED

Because the thick dividing lines in Fig.I.15 do not extend to the limits of the forest (the information collected is restricted), it is not possible to determine the exact area available for each group. However, if the dividing lines are elongated (interrupted thick lines in Fig.I.15), an estimate becomes possible for groups 2 and 4 whose location (near the forest edge) isolated them from other groups. The area of forest available to group 2 is around 25ha; of which 11ha were seen to be entered by marmosets (44%). The area of forest available for group 4 exceeded 40ha, of which 16ha were seen to be used (46%). It should however be stressed that the elongation of the dividing lines is artificial and may have produced an overestimate of the home range size.

There are few studies on wild C.jacchus and little is known about how the animals share a geographic area, or how variable are the home range sizes. Maier et al.'s (1982) and Stevenson's (1978)

estimates of home range size for C.j.jacchus are of less than 5ha, but these studies were conducted on very small remnant forests where troops may have been unusually packed. Data are not yet available for the other races.

Because different groups of C.jacchus may exchange agonistic vocalizations and displays, it has been thought that these animals are territorial (e.g. Maier et al. 1982 for C.j.jacchus). There are, however, descriptions of several family groups of C.j.penicillata sharing the same area, and even the same feeding-trees, separated only temporally (Lacher et al., 1981). At B.R. I did not observe encounters between groups, although twice I heard very prolonged bouts of loud vocalizations that could well have a spacing function. The intergroup behaviour probably depends on the local resources. At B.R., where there seems to be so much area available to each group, territorial behaviour should be infrequent.

DENSITY

On the basis of the area estimated to be available to groups 2 and 4, the density of marmosets at B.R. is around 15 individuals/km^2. C.j.jacchus have been reported to live in much higher densities (Maier et al. 1982, R.Hubrecht, pers.comm.). This could be due to ecological differences between the small affected areas where C.j.jacchus has been studied, and the much larger B.R. forest; there may also be physiological differences between races, as Thorington (1978) suggested: C.j.jacchus may be better adapted to a more degraded habitat. Since there are no other estimates of C.j.aurita densities elsewhere, it is not possible to evaluate the results

obtained. All that can be said for the moment is that the obtained figure is within the range of estimates for Callitrichidae density, i.e. between 10 and 20 animals/km^2. (Thorington 1978, p.7).

RELIABILITY OF RESULTS

Independence between Callithrix troops could not be established on the basis of simultaneous vocalizations (as in Callicebus) because their vocalizations cannot be precisely located beyond approximately 200m. For Callithrix, group independence could only be established if different groups were encountered at different places within a short period (i.e., short enough for one to be sure that the first group would not have had the time to move to the area of the second encounter). Encounters with marmosets were not very frequent, and even more infrequent were encounters with two troops within a short period. This casts doubt about the validity of Assumption B in App.I.4. If I failed to detect the independence between certain groups, the home range size indicated may be an overestimate, and the density indicated an underestimate.

There are, however, two facts that enhance one's confidence in the results:

a) the marmosets often vocalized at my approach (even if I had been unaware of their proximity); this prevents an observer from missing groups, and suggests that the small number of encounters was only due to the low population density.

b) marmosets at B.R. seemed to remain in restricted areas for several days at a time (see below); this increased my chances of sampling the various groups at that spatial position. This fact also helped strengthen some less firm indications of group

independence. For instance, on a given day I might have encountered two apparently independent groups, but the time of the encounters could not rule out the possibility of the first group having moved places; if in the following day I encountered marmosets in the area where I had first seen them, this would strengthen the two-group model.

USE OF THE HOME RANGE

Encounters with Callithrix occurred in clusters, both spatially and temporally; I often saw them in the same area two or three times within a period of two or three days, and then did not see them again for maybe several weeks. Although one cannot be sure without following the animals continuously, a possible explanation for this pattern is that the marmosets use certain parts of their home ranges intensively for a short period and then move to another area. This movement may be partly dictated by the plants' phenology. For instance, during April and May I saw marmosets more often than in the other months, and almost exclusively in vegetation type "B". It is tempting to associate this with the availability of the nectar from Mabea fistulifera flowers in that area at that time. I did not observe marmosets ingesting this nectar, but it was too obvious and abundant a source of energy to have gone unnoticed by them.

Inspection of Fig.I.15 shows that in certain parts of the forest the encounters were particularly frequent. To check whether in these areas the number of encounters was significantly higher than in the rest of the forest, I used the test already described in section I.2.6 (for the encounters with mammals). This test identified four one-hectare quadrats where the scores were particularly high (see

the stars in Fig.I.15). They are not all in one type of vegetation, but two of these hectares (see the two adjacent stars at the bottom left of Fig.I.15) involve the Astronium graveolens tree in which the marmosets were known to drill holes. For C.j.jacchus elsewhere, individual trees may be the centre of daily activities, the core area of the home range, and may be defended against other troops (Maier et al. 1982); this may also be true at B.R.

NOTES ON BEHAVIOUR

Behaviour across the day - Fig.I.16A shows that the Callithrix at B.R. were more often encountered late in the morning (day phase IV). They were not observed in day phase I and this could be an indication that they are late risers. These animals are probably more active in day phase IV; my restricted sample indicates that travel was more frequent at that time of the day.

Fonseca et al. (1980) found that for C.j.penicillata gum collection was primarily crespuscular, but at B.R. C.j.aurita were seen to feed on exudates at day phases II, III, X and IX (see Fig. I.16B).

Vocalizations - At least five different vocalizations could be recognized for the marmosets at B.R. A preliminary description of these calls and their context is given below.

VOC.1 - "Tss-kah" or "ti-kh"

In this vocalization one of these two syllabes can be emitted more than once, or be omitted.

Context: alarm, e.g. at observer's approach.

VOC.2 - twitter, very similar to a bird vocalization

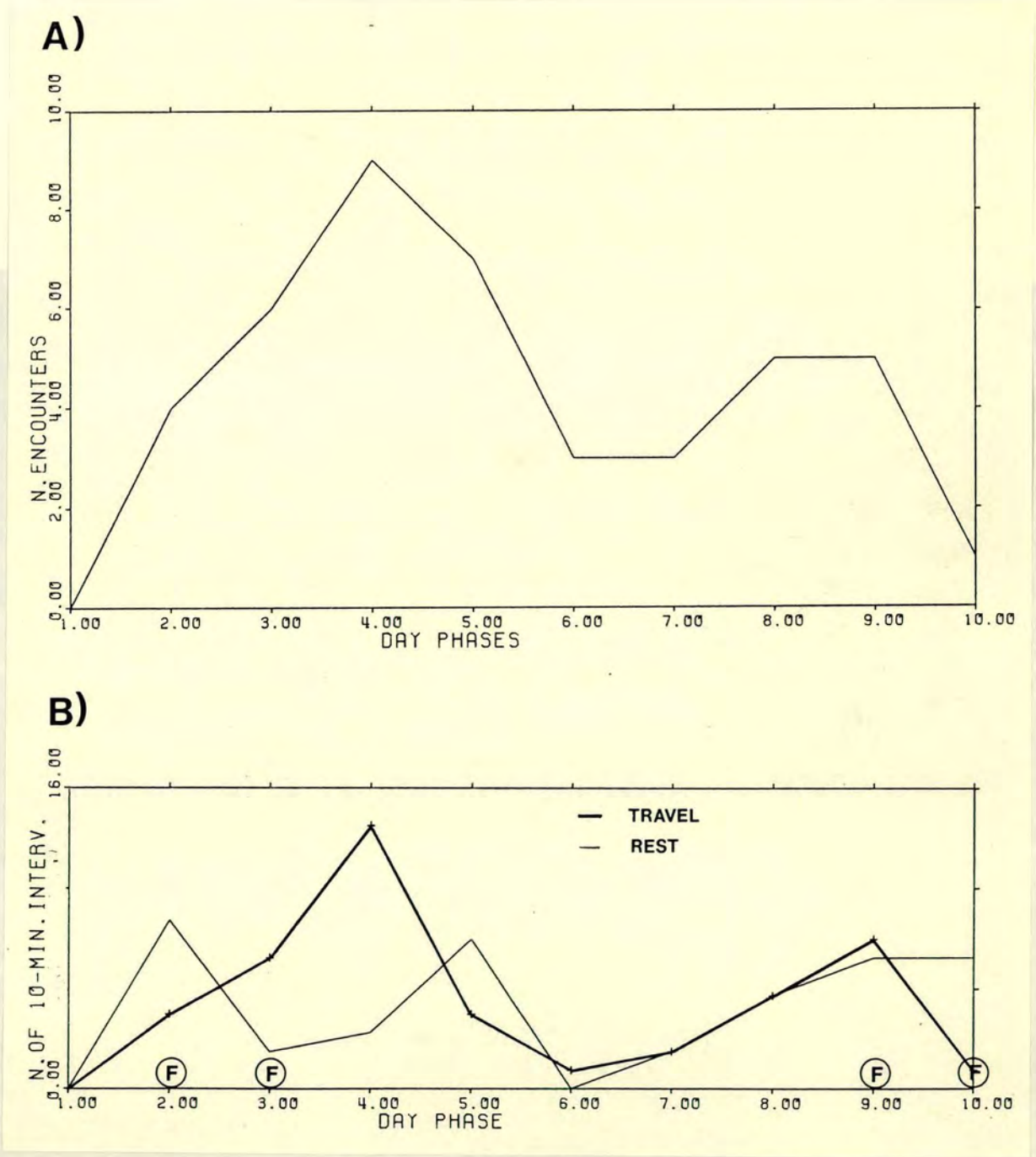
Context: social interaction (non-agonistic).

VOC.3 - whistles

Fig.I.16 -

a) Distribution of encounters with Callithrix across the day phases. (pool of data from the whole study period).

b) Frequency of Callithrix travel and rest across the day phases. "F" indicates day phases when Callithrix were observed ingesting tree exudates.



Data collected on 25 independent encounters indicated 8.4 ± 5.6m as the average height (and standard deviation) at which marmosets were found. This interval covers most of the forest vertical span. Although the marmosets can be seen at any height, they seem to favour travelling at low levels (less than 5m) and resting at higher levels.

The whistle is produced in several bouts, the first ones lasting around 1s, and the following ones becoming shorter, less loud and more staccato; this call may be exchanged intermittently between troop members for almost one hour, and can be heard for up to 200m.

Context: dispersed troop (travelling or not).

VOC.4 - repetitive cry

This vocalization seems to start with a whistle bout similar to Voc.3, grades into a very loud cry which is then repeated without the whistle; this vocalization can be easily taken for a bird's song, and may be emitted by several animals at the same time, without interruption, for 10-15min. It can be heard from 200+m, but it is difficult to locate the vocalizing animals.

Context: unknown; perhaps a spacing call.

VOC.5 - high frequency cry

This call may be a variation of the whistle. Context: unknown.

I.3.6 - CEBUS APELLA

NUMBER OF TROOPS

The number of Cebus troops in the intensive study area could not be estimated with the method in Appendix I.4 because its Assumption A is unacceptable (animals thought to belong to different troops shared areas). To estimate the number of troops in the area I used data on the location of known individuals together with indications of group independence. If more than one troop seemed to be in the intensive study area, I tried to identify them through the recognition of troop members. If this was not possible,

independence between groups was accepted only if they were quite separate (e.g. 300+m). This precaution is necessary because unrecognized individuals from the same troop may be 100+m apart and could be taken as independent groups. The reverse could also happen, i.e., two adjacent groups be taken for a single much-spread one.

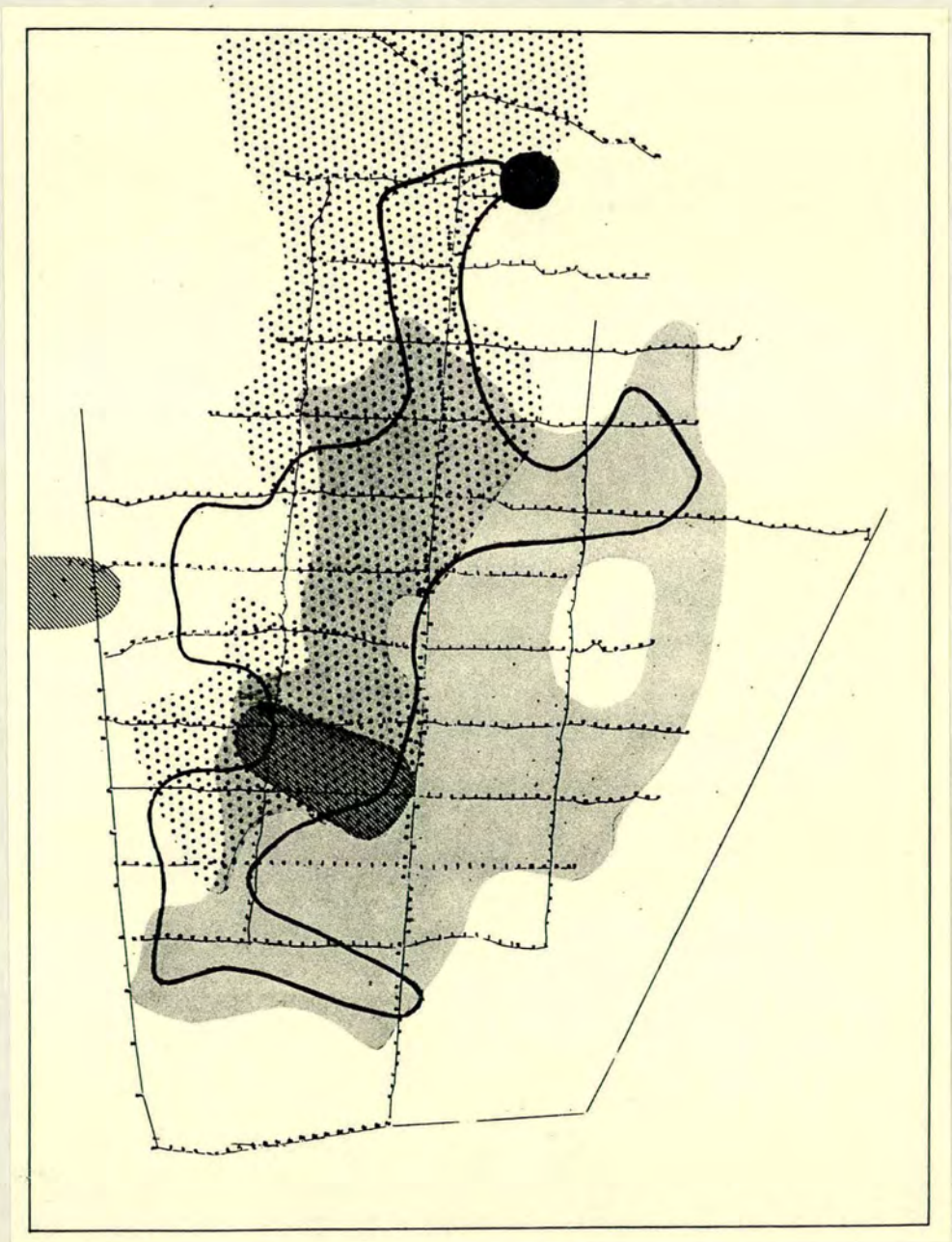
The information available indicates that five troops of Cebus can be found in the intensive study area. However, only two of these (the "Ceva" and "Porteira" troops) seemed to be permanent residents, since they were observed throughout the study period, whereas the other three were seen only occasionally (see last column of Table I.14). The "Campinho" troop entered the intensive study area regularly, but did not seem to stay there for more than a few hours at a time. To enter the study area this troop routinely descended to the ground and crossed a road at a traditional crossing-point. The "Calmo" troop was seen in the area for a few consecutive weeks and then was not observed any more. The "Briga" troop was seen only during two consecutive days, at the hunting hide.

Fig.I.17 shows the areas entered by the various troops.

TROOP SIZE AND COMPOSITION

At any encounter, one is likely to observe only part of a Cebus troop, since it generally spreads to such an extent that sub-units seem to lose contact. The best counts are possible when the troop is travelling or gathered to sleep. The troop size observed depended on the duration of the encounter. There was an increase in count size with increasing encounter duration ($r=0.72$, $n=38$);

Fig.I.17 - The observed home ranges of Cebus troops in the intensive study area. The trail network is the same as in Figs. I.5 and I.7. Two of the troops were seen less than four times ('Briga' and 'Campinho'); one was seen several times during a short period of less than one month ('Calmo'); the remaining two were seen throughout the year ('Ceva' and 'Porteira').



counts of 3 animals or less were generally the product of short encounters (less than one hour), and the largest counts were obtained during encounters of 4 hours or more. After 4h of contact the counts became reliable (the correlation between troop size and encounter duration for such long encounters is 0.22, n=15); different counts for the same troop, when the product of long encounters, should be due to other factors, like the temporary splitting of the troop, or infants leaving their mothers' backs, or even individuals changing groups. The best size estimates for each troop are given in the second column of Table I.14.

Recognition of age-sex classes was as follows: adults of both sexes generally have well developed hair tufts on the head; adult males are larger, stockier than females. Sub-adult males are almost as big as adult males, larger than adult females and their tufts are not very long. Sub-adult females do not constitute an easily defined class; this class was defined on the basis of incipient hair tufts, but museum material indicates that some of these females may be already able to produce young. The transition from juvenile female to adult female is probably a very quick one. Juveniles are slender, move independently from their mothers and do not have tufts. They frequently retain the infantile patch of dark hairs on the forehead.

Because the troop was rarely seen together, troop composition had to be studied by putting together information from different encounters. I started with the composition indicated by the encounter providing the best count, and then examined all other encounters with the same troop, adding to the troops' list all the animals not previously mentioned. For juveniles it was generally

TABLE I.14
SIZE AND COMPOSITION OF *CEBUS* TROOPS
AT 3 SITES IN THE STATE OF SÃO PAULO

SITE	TROOP	TROOP SIZE (best estim.)	COMPOSITION (*) (for site 1 composition was not obs.directly) ADULTS M	ADULTS F	SUB ADULTS M	SUB ADULTS F	JUVENILES	CARRIED INFANTS	N. ENCOUNTERS on which troop comp.is based, & THE N.MONTHS when the troop was seen
1)	Ceva	15	1	6	1?	3	2 or 3	Observed	15 (8 months)
	Porteira	13	1	4	1or2	1	6	Observed	16 (9 months)
	Calmo	13	1	7	2	1	2	Observed	8 (2 months)
	Campinho	8	1	2	-	1	2	Not obs.	3 (3 months)
	Briga	10	1	5	-	-	3	Not obs.	2 (1 month)
2)	Troop 1	12	2	3	1or2	2?	3	Observed	~3h each troop over a 4-day period. Good direct counts
	Troop 2	13	1	2	2	2	5	Observed	
3)	Pomar	15	2	6	-	4	3	Observed	~10h over a 5-day period.

(*) - may not add up to the estimated group size, which is based on animals either seen or heard.
(**) - infants may confuse troop counts; older infants often leave their mothers and may have been counted as juveniles.

Sites:
1 - Barreiro Rico, site B in Fig.I.2
2 - Gália, site A in Fig.I.2
3 - Lageadinho, site C in Fig.I.2

impossible to decide whether an individual had been seen before or not, so for this category the accepted number is the maximal count. The troop composition obtained for the various troops at B.R. is shown in Table I.14, which also provides comparative data from two other sites near B.R.. This table shows that the sex-ratio in the adult class is imbalanced; at B.R. all troops seemed to have only one adult male for at least 4 adult females. At the other sites two adult males lived (peacefully) in the same troop, but the sex-ratio was still imbalanced. This is to a certain extent due to delayed maturation of males, but may also be reflecting differential mortality or the tendency of males to leave the troops. At B.R. on two occasions I observed what seemed to be bachelor cohorts comprising two adult males.

The troop size and composition observed for C.apella during this study are within the range observed for the species. Small troops of 4 or 5 animals have been reported. Some of these may be underestimates caused by the non-cohesiveness of C.apella troops. Where detailed work has been done (e.g. Izawa 1980, Janson (in prep.)), the reported troop size tends to be 10 individuals or more. Almost all studies on C.apella indicated that there are fewer adult males than females in the troop, although more than one adult male per troop seems not to be rare. A list of troop size and composition for Cebus is given in Freese & Oppenheimer (1981). Additional information is found in Izawa (1980) and in Janson & Terborgh (in press).

AREA OCCUPIED

The three troops that seemed to be occasional visitors to the

intensive study area were seen only in hectares also used by other troops. Although these troops may roam over a large part of the intensive study area, their centres of activity (core areas) are probably somewhere else. For the two resident troops, the following was observed:

TROOP	N.OF HECTARES SEEN TO BE USED	N.OF HECTARES OF EXCLUSIVE USE
"Ceva"	51	21 (41%)
"Porteira"	54	17 (31%)

The figures above would probably be altered with further observation. For the 'Ceva' troop the home range is surely larger than indicated, as this troop was seen to move outside the intensive study area.

There is some information on home range size for C.apella troops at Amazonian sites: for Vichada, E.Colombia, Defler (1979A) indicated 100ha, and Janson & Terborgh (in press) estimated 80-90ha for the C.apella of Manu, Peru. At Manu almost no area was used exclusively by only one troop, but few areas were used by more than two. At La Macarena, Colombia, the Kleins (1976) found that 4 to 6 troops occupied 3 square miles. This would be equivalent to around 120ha for each troop, if troops divided the area equally among themselves, but other work in the same area (Izawa 1980) indicated that the home range of one troop was around 300ha (deduced from his Fig.3). Izawa indicated that there are 4 or 5 troops in his total study area of around 530ha (estimated from his Fig.1),so there must be almost total overlap between the ranges of different troops. At Gália (site A in Fig.I.2) I observed at least two C.apella troops

obtaining corn from the same hunting hide, which indicates home range overlap. The two troops could be seen at the hide in the same day, but not at the same time.

More examples will be needed before generalizations are made, but the cases studied so far indicate that, although there may be areas of exclusive use in C.apella's home ranges, these tend to overlap extensively. C.apella does not seem to be territorial in the sense described for C.capucinus (Oppenheimer 1968) and for C.albifrons (Defler 1979b).

DENSITY

Because of the type of overlap between the home ranges of different troops, it is difficult to define Cebus density at B.R. If all five troops used the intensive study area equally, and this area constituted the whole of their home range, the density would be approximately 50 indiv./km^2. If only the two resident troops occupied the intensive study area, and this comprised the whole of their home range, the density would be around 25 animals/km^2. The real figure depends on how much larger are the troops' home ranges and on the spatial and temporal overlap between home ranges.

There are no other density estimates for C.apella in Atlantic forests. For Manu (Peru) Janson & Terborgh (in press) estimated that the C.apella density was between 20 and 35 indiv./km^2. (the value depends on the method used, and they used several to compare between them). The information provided by Izawa (1980) corresponds to approximately 15 indiv./km^2 at La Macarena (although this figure was deduced by me, and is not mentioned by Izawa). Branch (1979) estimated that 1 or 2 groups occupied a square kilometer (i.e.,

between 18 and 36 individuals/km^2, since the average of her best counts was 10 ind./group). Other less detailed studies yielded values between 15 and 55 indiv./km^2. (see Freese and Oppenheimer 1981). Considering the difficulties in estimating group size, home range size and home range overlap, and also the probable ecological differences between sites, these figures are not too variable, and the B.R. results are within the observed range.

RELIABILITY OF RESULTS

The results presented on troop size and composition were collected at different times during an encounter, or from different encounters with the same troop. Such a technique is based on the following assumptions:

1. the troops had fixed composition during the study period;
2. the troops did not mix;
3. my descriptions of the animals were sufficient to identify them.

Assumptions 1 and 2 are reasonable, although not certain. In this respect, the main difficulty was that troops could be separated by a few hundred meters without showing any open agonism (they might have been unaware of the presence of the other troop). If I walked into the second troop and did not recognize individuals, I might add animals from troop 2 to the list of troop 1. I avoided this type of error by using only data from encounters which I was sure involved only one troop (as confirmed by re-sighting known animals). As for the third assumption, I used only the cases where I had confidence about the animals' identity, but misidentification remains a possibility.

In spite of the artificiality of the method used to compose the

troop, the obtained results do not conflict with the results obtained at Ourinhos and Gália (table I.14), where the counts were direct and reliable.

USE OF THE HOME RANGE

To investigate whether Cebus frequented all parts of their known home range to the same extent, the following method was used. Only the best sampled troops (Ceva, Porteira and Calmo) were considered. Each encounter was divided into 19-minute intervals (19 minutes is the average time a Cebus needs to cross a one-hectare quadrat). At each interval the location of the monkeys was noted, and one score was given to each hectare entered by at least one monkey. The expected number of scores in each quadrat (i.e. corrected for differential sampling) was calculated as explained in Appendix I.7. The quadrats where Cebus were not seen were not considered because I wanted to determine only whether there were quadrats that were preferred among those entered. The deviation from the expected values was then calculated. (see Appendix I.7 for the actual scores and also for the location of these quadrats of high deviation). Apart from the hectare containing the hunting hide, with is obvious attraction, the hectares favoured by the three troops show a tendency to concentrate in roughly the same area. For troop 'Calmo', which seems to be an occasional visitor, the favoured hectares are mostly in vegetation type B, and in this case the preference could be partly due to the existence there of food items exclusive to vegetation B. However, this troop did not use all area B equally, but favoured hectares which were also preferred by another troop ('Ceva'), which did not seem to have any special

vegetation feature. The two resident troops clearly favoured that same area, but the hectares where each troop was more frequent are not the same - they are adjacent. This area is also the furthest place inside the intensive study area where the 'Campinho' group was seen to go (Fig.I.17), and there I heard prolonged exchanges of loud vocalizations between what I believed to be two troops. It seems that in this area intergroup interaction is particularly frequent, although the nature of such interaction, and the reason why this area is preferred over others, are not clear to me.

NOTES ON BEHAVIOUR

Cebus were observed more than the other species and I was also more familiar with their behavioural repertoire, so the information collected on this species' behaviour is disproportionately more abundant and diversified than for the other species. Comments are restricted here only to the following two striking features:

Apparent lack of troop cohesiveness - although the associations between individuals seem to be stable and troops do not seem to mix freely, the internal cohesiveness of troops is not generally evident. A Cebus troop typically spreads out, its members either associating into smaller units or remaining alone. Smaller units often consist of groups of lactating females, or of juveniles, or adult male with juvenile(s), or a female with (supposedly) her two latest offspring.

Individuals or sub-units may become isolated from the rest of the troop without showing signs of distress. Likewise, the main body of a troop does not necessarily wait when sub-units or individuals lag

behind. At night the troop may or may not use a single tree. The latter seems to be more common.

With these characteristics, and the extensive overlap of the home ranges of different troops, it would be surprising if the troops did not exchange members occasionally. Janson (in prep) suggested that male cohorts in C.apella cannot be considered as being isolated. I would expect that C.apella troops are less stable than territorial species.

Complex communication - Although out of sight of the rest of the troop for a large part of the day, the members of a Cebus troop often communicate vocally. There is some indication that the animals are able to discriminate between calls given by different individuals. Cebus calls do not carry over long distances like those of Alouatta or Callicebus, but some vocalizations can be heard up to 300m away and this occasionally indicates to the animals their proximity to another troop. C.apella's vocal repertoire includes contact calls (more than one type), alarm calls (more than one type), fear screams, aggressive staccato shrieks, infant trills and submissive twitters. Most of these vocalizations have variations depending on the animal's arousal, and some grade into others. Animals were occasionally fooled by humans imitating their contact calls, but more often they replied with alarm calls. The social interactions between animals in visual contact may be very complex and involve subtle and quick signalling. Signals and responses are often so quick that cannot be properly observed without video equipment.

I.3.7 - ALOUATTA FUSCA

NUMBER OF TROOPS

As already mentioned in section I.3.2.2, the method described in Appendix I.4 was not suitable for Alouatta; it produced reversals, indicating that the assumptions did not hold for this species. The most likely difficulty is to assume that the area entered by a given troop is for its exclusive use. Milton (1980B) and Chivers (1969) showed that there is overlap (up to 100%) between the home ranges of A.palliata troops at Barro Colorado Island. Carpenter (1965) stated that these howlers did not defend boundaries or whole territories, but defended the place where they were. Chivers (1965) also suggested how the home range size and the degree of overlap changed according to population pressures.

Although no comparable study is available for A.fusca, overlap of home ranges could also exist at B.R. and cause the reversals mentioned. To analyse the A.fusca data it was necessary to use a method that, instead of imposing a spatially fixed home range, allowed the troops to shift their position and maintain distance from neighbouring (vocalizing) troops. An alteration of the method in Ap.I.4 allows for this, based on the following principle; even if shifts occur, over short periods these shifts are small (howlers are slow moving and rest most of the day), so that the resulting spatial picture is similar to that of territorial species. By inspecting the spatial pattern at consecutive periods, one should be able to follow the change in the relative position of troops, although the

superimposition of all the patterns might not make sense. In an attempt to identify spatial patterns within limited periods, I divided the data into four sets, each containing the information from three consecutive months. Smaller sets could not be used because a preliminary inspection of the data suggested that general patterns would not emerge if the data were further divided. Besides dividing the data into sets, the procedure described in Appendix I.4 was further modified: within each set the information was examined in its chronological sequence and not in the order used for the other species (i.e. from the case showing the largest number of independent groups to the case with the smallest). Also, instead of plotting only the cases which indicated group independence, I plotted the location of any howler group whose location I knew, in an attempt to follow the movement of each group. At each plotting new home range circles were drawn around the spot, and the old ones were discarded. Even if the sequence of troop movement was often interrupted (I did not go to the forest every day), the procedure of transferring home range circles was necessary to prevent an overestimate of the population as troops moved out of their original home range circles.

Because Alouatta vocalizations may carry over 700m, groups that did not live in the intensive study area could be heard from within it. As in the case of Callicebus, I assumed that the roads around the intensive study area were natural boundaries between home ranges.

The modified method produced consistent results (Fig.I.18). Although the number of independent groups indicated by each 3-month set varied between 5 and 7, the discrepancies were caused by the more remote groups. In the intensive study area itself, each

3-month set indicated the existence of four independent groups.

TROOP SIZE AND COMPOSITION

It takes hours to obtain reliable counts (Fig.I.19) of Alouatta troops, because these animals remain immobile for long periods and individuals are easily missed. Therefore when I saw a group I was generally unsure whether it was a new troop or part of a known one. The most reliable counts indicated that the troop size varies from 4 to 11 independently locomoting animals. The extremes correspond to counts made at quite distant places in the intensive study area (respectively top and bottom of Fig.I.19), and should correspond to different troops. Their composition was:

Largest troop -

- 1 adult male
- 1 sub adult male
- 4 adult size females (two of them breeding)
- 1 individual of female adult size (sex not confirmed)
- 2 juveniles (sex?)
- 2 infants (sex?)

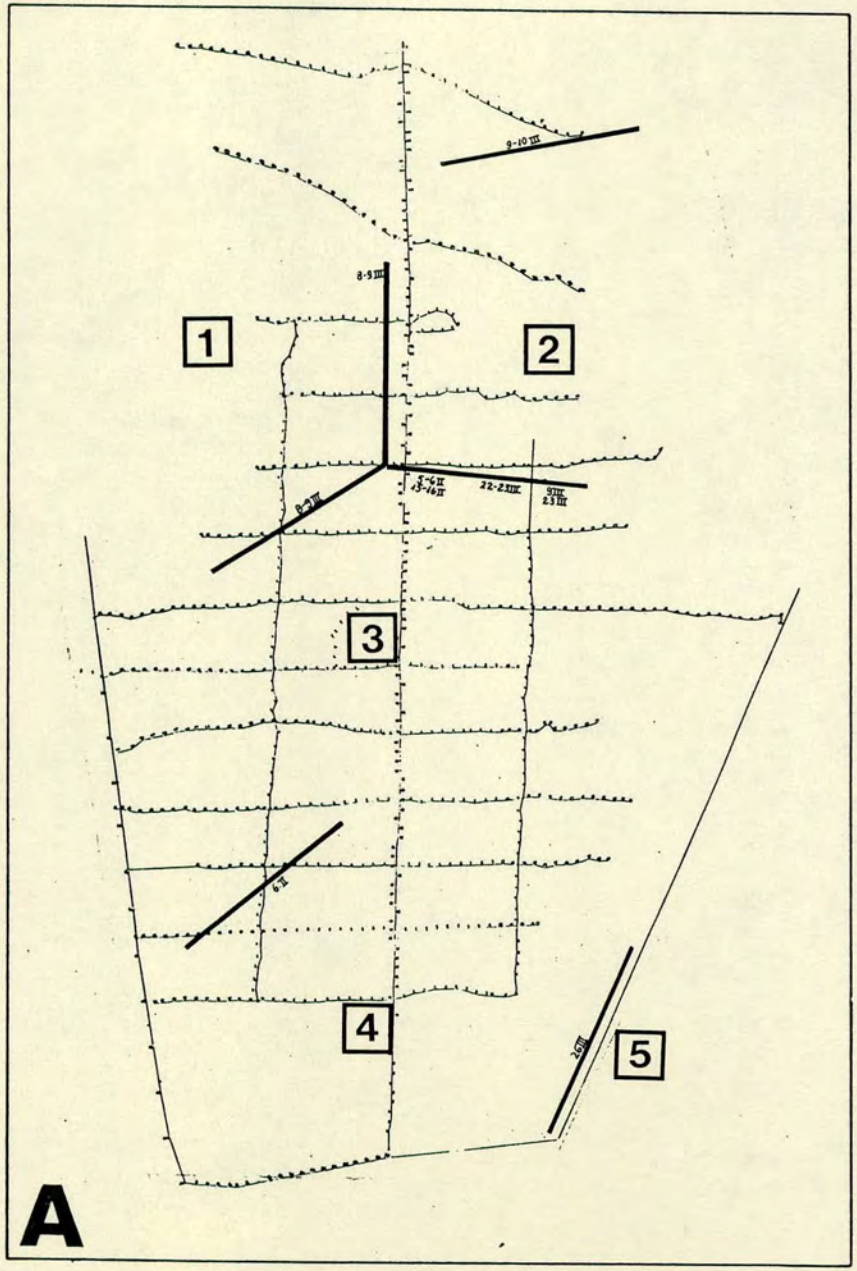
Smallest troop -

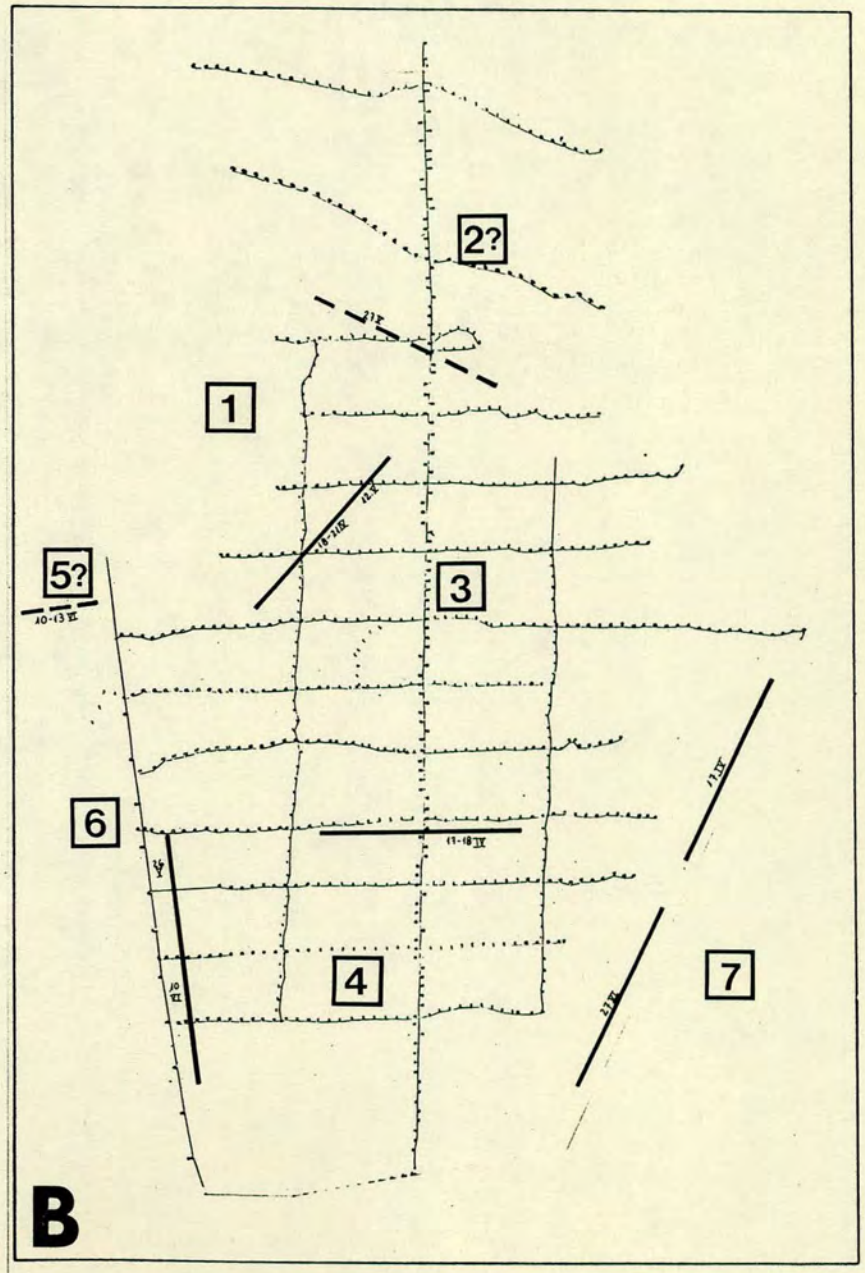
- 1 adult male
- 2 adult size females (one of them breeding)
- 1 infant (sex?)

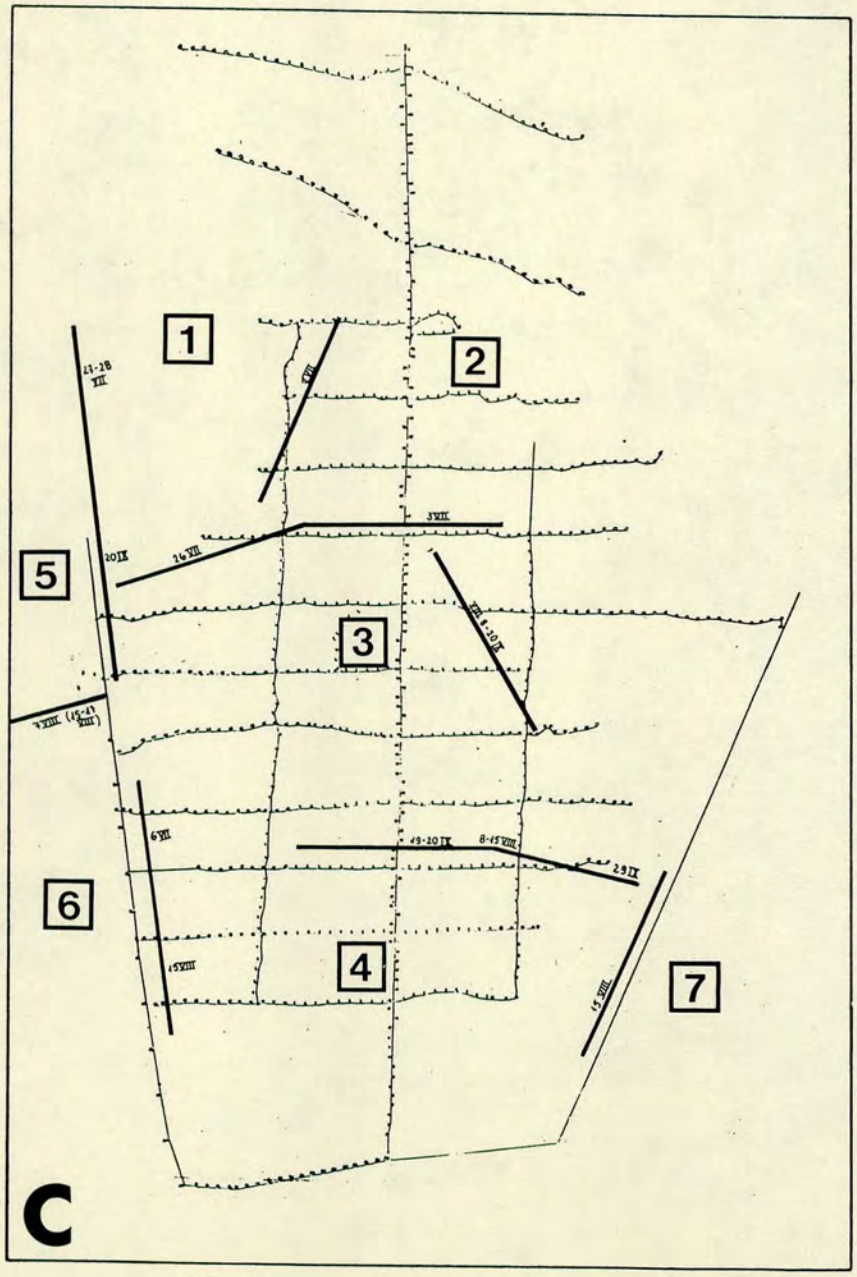
Adult males are red and easily recognizable. Adult females and young are dark brown, although some females (old?) may have golden coloured tips of tails and nape. The genitalia of immature animals is very evident, whitish, globose, (reminiscent of white testicles) and seem to be similar in both sexes. Breeding adults do not have whitish genitalia. On only one occasion did I observe more than one adult male in a troop, and this troop seems to have then split, separating the two adult males. On one occasion I saw a group

Fig.I.18 - The independent groups of Alouatta fusca suggested by each of the 3-month data sets (details in the text). The numbers within the squares are not troop identifiers, although for the groups within the intensive study area (groups 1 to 4) they may well correspond to the same troop in all drawings (see Fig.I.19).

A - Jan. to Mar.
B - Apr. to Jun.
C - Jul. to Sep.
D - Oct. to Dec.


1
2
3
4
5
A


2?
1
5?
3
6
4
7
B


1
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C

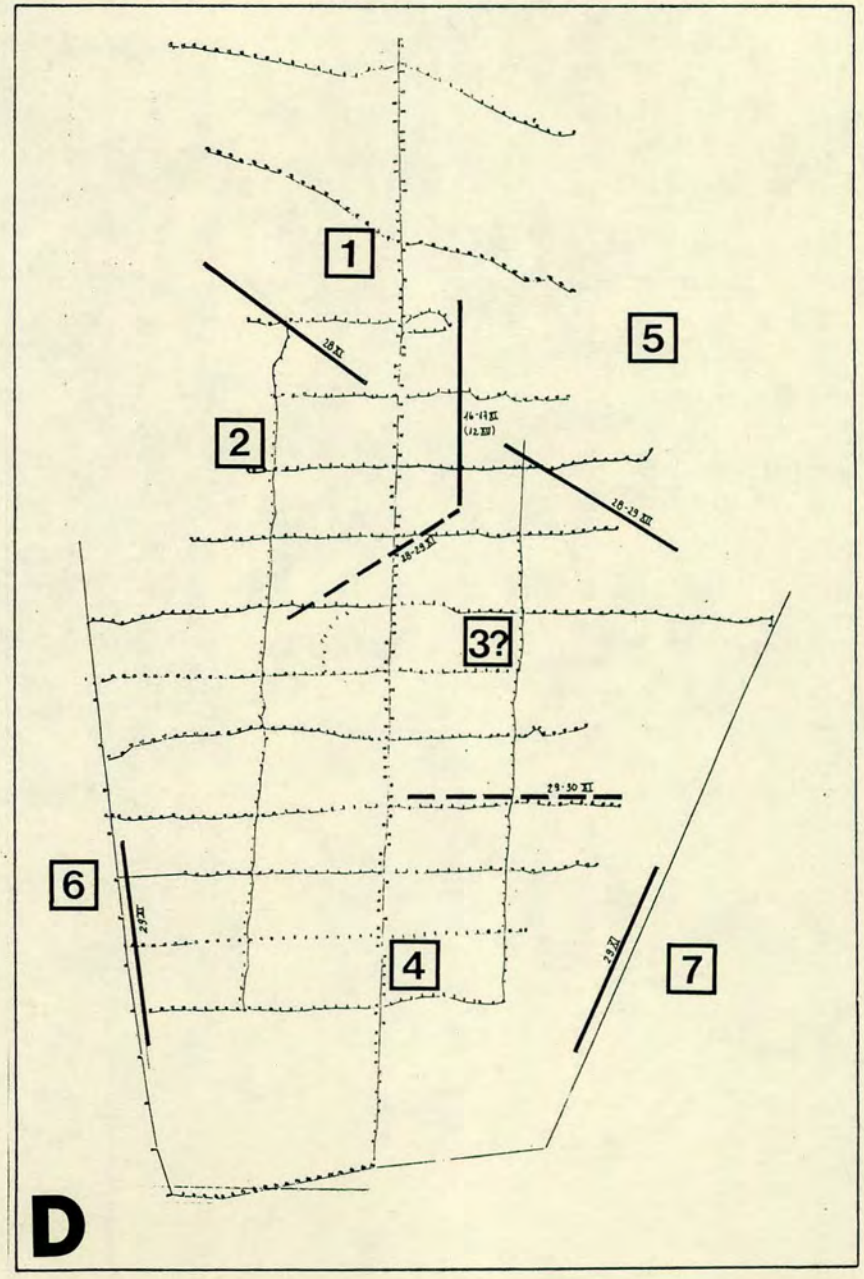
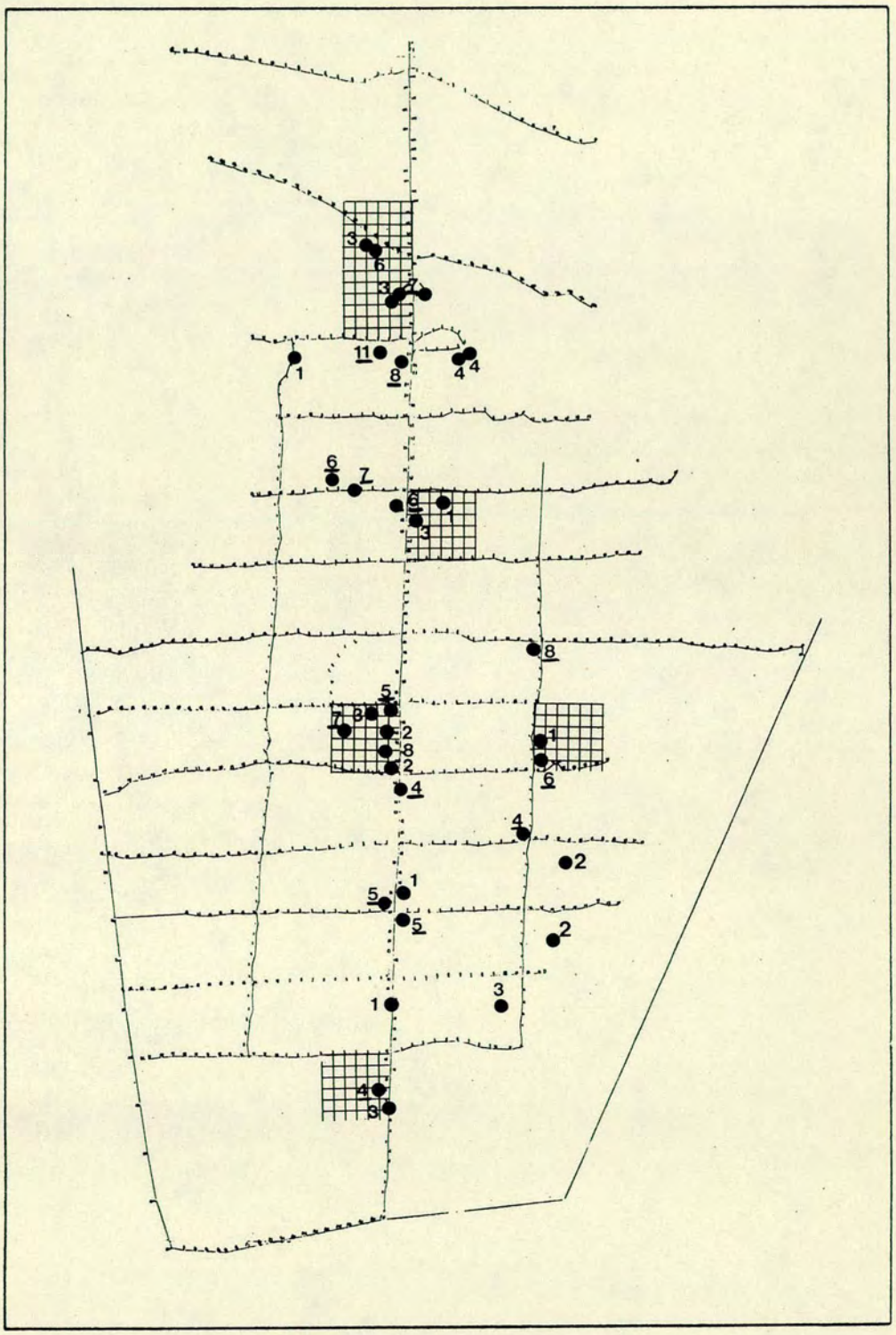

1
2
3?
4
5
6
7
D

Fig.I.19 - The location of encounters with Alouatta fusca are marked with black dots. The numbers indicate how many animals were seen during that encounter. The most reliable counts are underlined. In spite of group size variation, large groups (i.e. more than 8 animals) were not observed in the bottom part of the figure; also, some group sizes are repetitive in some places, suggesting that the same troop was encountered more than once at the same place. The hectares that had a high number of encounters ($p<0.05$ in Poisson distribution) are shaded.



consisting of two maturing (reddish brown) males exchanging vocalizations with the adult male of a nearby troop. The information above suggests that the imbalance of the sex ratio in the adult class is due to maturing males leaving the troop.

At other sites of S.Paulo State where I observed A.fusca, troop size and composition seemed to be similar to that observed at B.R.; almost all troops had only one red male, and varied between 5 and 12 individuals; Cantareira (D in Fig.I.2): 5 to 8 ind./troop; Lageadinho (C in Fig.I.2): 6 to 12 ind./troop).

AREA OCCUPIED

It is not possible to know the home range size of the troops at B.R. since they were not followed. If the intensive study area was to be divided among its four troops, at least 29ha. would be available for each troop. Since it seems that the home ranges overlap, each troop is likely to use more than 29ha. At another site (Lageadinho), however, A.fusca was observed to live much more packed, each troop having the equivalent of 7ha. or less; due to the size and shape of Lageadinho forest, even allowing for home range overlap, its troops are unlikely to have home ranges of the size possible at B.R.

Variation occurs also in other species. Milton (1980B) indicated that each of the two troops of A.palliata she studied at Barro Colorado used ca. 31ha. (troop size:18), whereas Glander (1978) indicated that a troop of the same species in a gallery forest in Costa Rica used approximately 10ha. (troop size:13). In the last case the forest was narrower and more restricted than at B.C.I.

Several factors are probably influencing the size of the area used by a troop: the species typical troop size, the type of forest

involved (e.g. whether semideciduous or not, whether on good soil or not), its shape, and the Alouatta density. More studies on the same species in different habitats are needed before generalizations can be made.

DENSITY

Using the 10 best counts for B.R. troops, the average group size is 6.4; this yields a density of 22 ind./km^2 in the intensive study area. If all groups were of the smallest observed size, density would be 14 ind./km^2 and if they were of the largest size, density would be 38 ind./km^2.

A.fusca can be found at much higher densities. Silva (1981) estimated the density at Cantareira to be 80.9 ind./km^2, but thought that this could be an overestimate. At the 48ha Lageadinho forest I counted at least 47 animals, which yields a minimum density of 98 ind/km^2.

The density of A.palliata is also known to vary a lot, not only between sites but also within a single one. At Barro Colorado it seems to have oscillated drastically since the first studies in the 1930s, the number of individuals varying from 237 in 1935 (Carpenter 1965) to at least 926 in 1967 (Chivers 1969). For an island of 4000 acres (value given by Oppenheimer 1968) this corresponds to oscillations from 17 to 65 ind./km^2 (the values are probably higher, as unsuitable habitats have not been deducted from the total island area). Even if some of the variation is due to differences in censusing methods between studies, the differences are of such a magnitude that it must be reflecting, at least to a certain extent, real oscillations. An epidemic has been invoked to explain the low

densities found initially at B.C.I. The same could have happened in areas occupied by A.fusca, (Laemmert et al. 1946), but density is also probably determined by forest type. B.R. is on a relatively poor sandy soil that is unable to retain water. The forest is semideciduous and there are seasonal stresses. Both Cantareira and Ourinhos (where density was high) are on better soil and do not seem to suffer serious water stresses.

RELIABILITY OF RESULTS

The validity of the data presented on the size of Alouatta population at B.R. depends on the reliability of the estimate of the number of groups in the intensive study area. The method used provides a minimum figure. It accounted for the probable home range overlap, but an assumption remains: that the independence between all troops had been recognized. If a troop was observed on one day but failed to vocalize the following day(s) when its neighbour did, I would assume, if I had no more evidence, that the first group had moved to the place from where I heard the call. This would produce an underestimate of the population. However, if Alouatta vocalizations have indeed spacing purposes, it would be unlikely that troops would consistently remain silent, particularly when the nearest neighbours vocalized. Overestimates of the population are unlikely, since this could only happen if I admitted two troops where there was in fact only one that had moved; as the area attributed to each troop is the average home range size (as from the literature) to move out of it and back again to fit the observations, the animals would have to be far more mobile than they seem to be. The figures are therefore more likely to be

underestimates, but probably not a very serious one. It is certain that the density at B.R. is lower than at the other sites visited; this is indicated by the higher frequency of encounters at Cantareira and Ourinhos and also by the relatively low frequency of vocalizations at B.R. (see below). This may be an indication that at B.R. the Alouatta population does not need to broadcast their location so often.

USE OF HOME RANGE

The distribution of the encounters in the intensive study area indicates that some parts of it are preferred to others. Fig.I.19 shows the places in the intensive study area where Alouatta were seen, and the six one-hectare quadrats where the number of encounters was so high as to be associated with $p<0.05$ in a Poisson distribution (same method as used for Callithrix and Callicebus). Three of these quadrats contained sleeping trees, but these may be there simply because the quadrats are favoured, and not the other way around. Milton (1980B) found that the A.palliata at B.Colorado did not have special sleeping trees, their activities being centered around pivotal feeding trees. At B.R. the favourite quadrats are not restricted to one type of vegetation, and in none of the cases there seemed to be a particular tree attracting the animals. It is tempting to associate some of these favourite areas with the core area of different troops' home ranges. The number of animals seen in each provides some support for this idea, but this would require more direct observation.

NOTES ON BEHAVIOUR

The most obvious feature of Alouatta's behaviour is their roaring calls. The A.palliata of Barro Colorado Island (B.C.I.) were the first to be studied and their 'dawn chorus' has been often mentioned in the literature. Carpenter (1965) and Chivers (1969) quantified the roars emitted by B.C.I. howlers across the day and showed that there was a very marked peak during the two hours around dawn. After that period the frequency of roars dropped to ca. 13% of the peak frequency and remained low for the rest of the day (figures calculated from the graph in Carpenter 1965). Chivers demonstrated the same peak using a slightly different measure: the number of days on which calls could be heard at a given time. His data showed that in a given day an observer had 80+% chance of hearing calls around dawn. As the day went, this chance decreased, being at most 40% and generally less than 29%. I applied both methods to the B.R. data; both methods give similar results, but I will consider only the results obtained with Chivers' method (Fig.I.20) since for populations where calls are relatively infrequent (as in B.R.) Chiver's method is more conservative (less affected by a few particularly long calls). When data from the whole year are pooled together (this assumes that the pattern is the same all year round), two main differences between B.R. and B.C.I. become evident. First, at B.R. the calls were less frequent. Second, at B.R. there was an increase of calling as sunset approached (day phases IX and X). Although at B.R. the highest peak was also at day phase I, these early calls were heard only on ca. 20% of the days, and not on 80% of the days as in Chivers' sample. Similarly to Chivers' data, at B.R. there was a decrease in the probability of hearing calls after day phase I, but the minimum was ca. 7%, instead of Chiver's 18%.

The difference in overall frequency of calls could be due to A.fusca being less vocal than A.palliata, but could also be a function of density: Chivers estimated that 14ha were available for each troop at his study area, and there would be 29 or more for each troop at my site.

When data from the rainy and the dry season are separated, different trends seem to appear in each set. The pattern described by Chivers for B.C.I. (his sample was taken at the start of the wet season) does not match B.R.'s wet season pattern; it would be more similar to B.R.'s dry season pattern. These apparent seasonal differences did not prove significant ($X^2=7.3$, d.f.=4, $0.20<p<0.10$), but the sample is small and it cannot be ruled out that there are not differences between seasons. If only the morning had been considered, the results would probably be significant. In any case, the results obtained at B.R. indicate that generalizations should be avoided. The frequency of calling may vary widely between sites, and their distribution across the day is not always so dawn biased as one would expect from the customary term "dawn chorus". Just as has been said for Callicebus, in Alouatta there may also be species-specific differences in the timing of calls, or this may be a function of the atmospheric conditions (Quine 1981).

At B.R. Alouatta vocalizations seemed to be emitted more frequently from certain places, but due to the uncertainties in the distance estimates, the obtained pattern is not really reliable.

Vocalizations are emitted primarily by the adult males. The other members of the troop sit silently in the vicinity, and only occasionally does another troop member call with the male. In contrast to a male's, a female's vocalization is hardly audible. On one occasion I saw a sub-adult

Fig.I.20. - Distribution of Alouatta long-range vocalizations across day-phases. Pool of data from 1979. Number of sampling days:103 (rainy season: 50; dry season: 53).

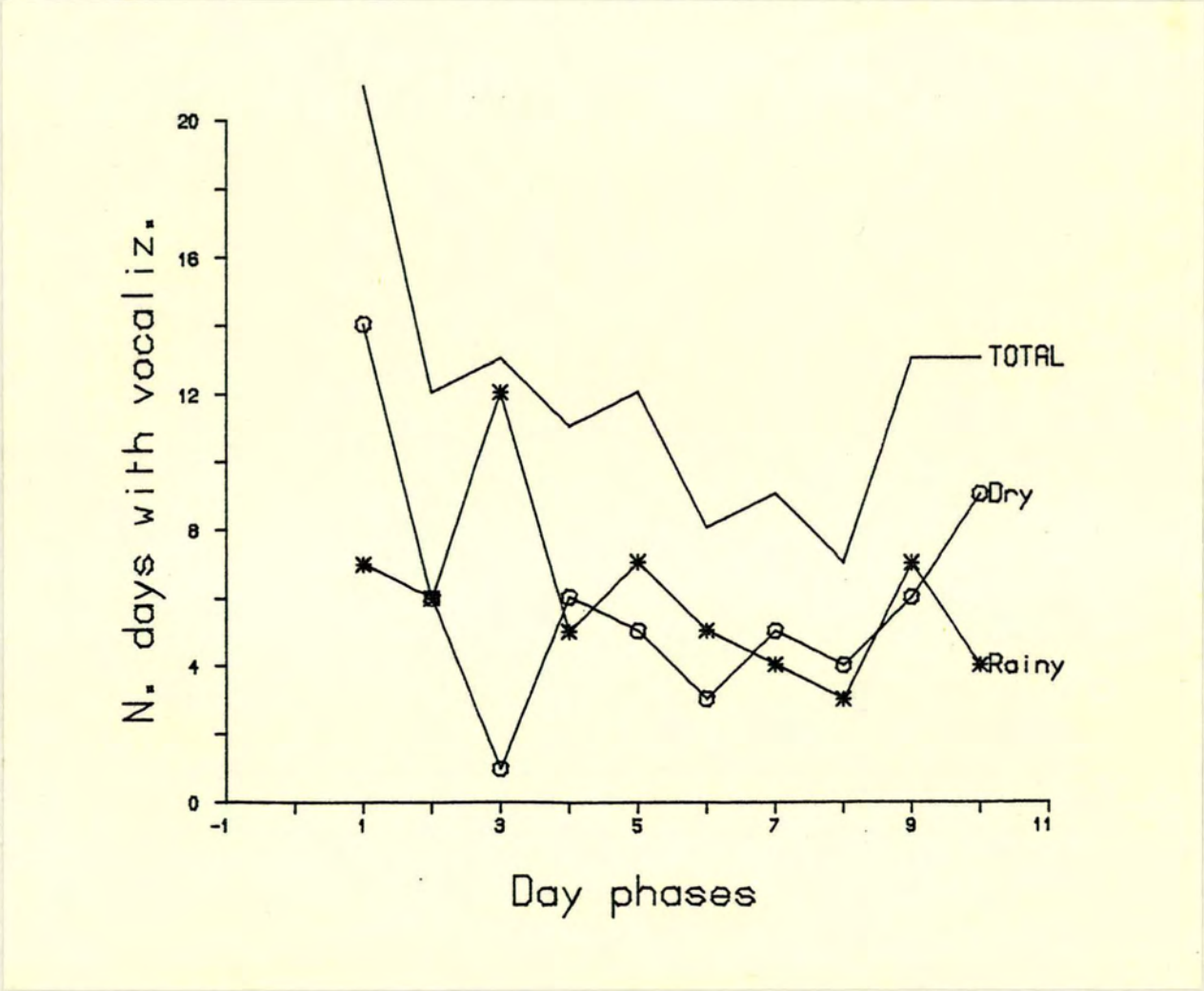
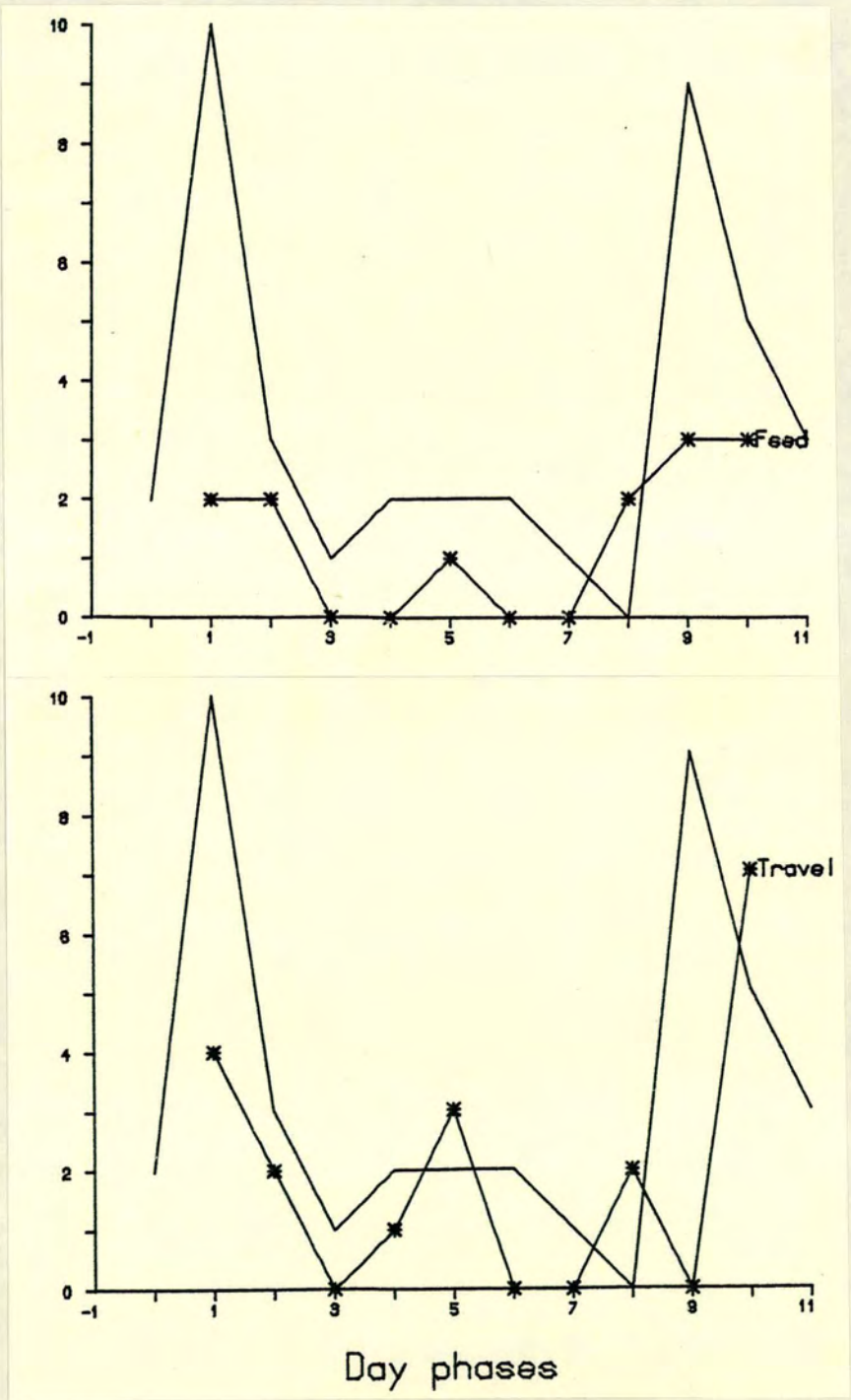


Fig.I.21 - Distribution of encounters with Alouatta fusca across day phases, and its relationship with their travelling and feeding. Travelling and feeding were measured in number of 10-min intervals during which at least one animal was seen to perform the behaviour in question. Pool of data from 1979.



male "doubling" the adult male of the troop during a calling bout: the sub adult inhaled and exhaled in a rhythmic fashion, kept his mouth open as if emitting a roar, but produced no audible sound.

At B.R. I encountered Alouatta more frequently early in the morning and late in the afternoon. This is probably associated with their tendency to travel at those times, which in turn is associated with feeding bouts. (Fig.I.21).

I.3.8 - CONTACT BETWEEN THE PRIMATE SPECIES AT B.R.

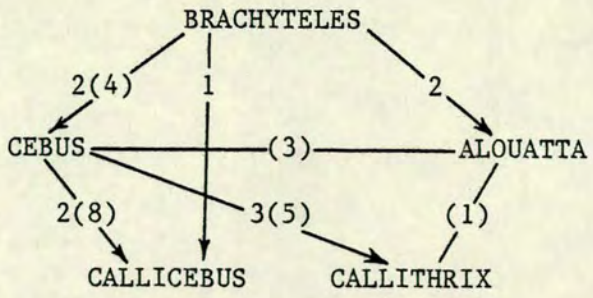
It has been shown that the five B.R. primate species coexist in the intensive study area. There was no indication that any species were restricted to areas where others were absent. Each species is expected to meet all the others, but the frequency with which this happens depends on each species' density, travelling speed, home range size and travelling behaviour. Some information on these topics has been provided in sections I.3.3 to I.3.7, but the modelling of the expected number of encounters between species (like the "perfect gas" model of Waser 1982) requires more detailed information. Nevertheless, it can be predicted that Brachyteles and Cebus (particularly the more abundant Cebus) encounter the other three species more often than these three encounter one another. This is because Brachyteles and Cebus travel much faster than the other species (see table below), their home ranges encompass several of the other species', and also because the other species seem to occupy areas that they cannot cover in a short period.

AVERAGE (NOT MAXIMAL) TRAVELLING SPEED
FOR THE PRIMATES AT B.R.

Species	Speed:	N.of travel instances used for the average (*)
Brachyteles	450 m/h	8 (selected)
Cebus	380 m/h	26 (selected)
Alouatta	210 m/h	4 (selected)
Callicebus	190 m/h	10 (non-selected)
Callithrix	150 m/h	6 (selected)

(*) Not all instances provided comparable information on travelling speed. The estimated speed could be very reliable (e.g. when a set of known individuals was followed continuously during a travel bout),or could be imprecise (e.g. when the travelled distance was small as compared to the group spread). To improve the estimate, only the best evidence was used.
For Callicebus no selection was possible; there were few indications of travelling and all were used.

I observed some encounters between primate species at B.R. While some did not suggest that any one species could routinely displace any other, a few did. Aggression between species was not observed, but avoidance was. On the basis of which species avoided which, a coarse hierarchy can be established between species. Such a hierarchy is represented below, with rank decreasing from top to bottom. Arrows point from avoided species towards avoiding species. The number of avoiding instances is indicated near each arrow. Numbers between brackets are the number of encounters with no evident agonism. For some pairs of species I have no information.



The data above suggest that at B.R. the larger species may displace the smaller ones. However, characters other than body size may also have an influence on the outcome of an interspecific encounter. For instance, Cebus may occasionally displace and chase the larger Alouatta. This was not observed at B.R. but at Ourinhos, see Fig.I.2, where I observed one adult male C.apella threaten and displace a group of two adult females and one adult male of Alouatta fusca. Also, Miranda Ribeiro (1924) reported an instance of C.apella attacking and injuring Alouatta fusca.

In spite of the agonistic instances mentioned above, the relationship between primate species at B.R. is more aptly described as indifferent, or neutral. There was no overt aggression between species, but neither did I observe any polyspecific associations (of the type described by Klein & Klein 1973 or by Gautier & Gautier-Hion 1969). On several occasions troops of different species were known to be within 100m of one another, or within hearing distance, without individuals of either species showing any striking reaction. In most cases they were not within sight of each other.

I.3.9 - NOTE ON CONSERVATION

Perhaps the most important result on the primate population at B.R. is the indication of relatively low densities for Callithrix, Callicebus and Brachyteles. For the first two species this is surprising since other species in the same genera have been reported to live at much higher densities. There are many possible explanations for these low densities: possible recent epidemics, high mortality after particularly heavy frosts, competition with the sympatric fauna, annual bottlenecks caused by the dry season, or others. Much more detailed work would be necessary to identify the constraints acting on the B.R. primate population.

Whatever the cause, it is important to realize that the absolute numbers of Brachyteles, Callithrix and Callicebus are very small, and that the removal of even a few individuals could have a serious impact on the population, particularly for the last two species where there is a single breeding female per social unit.

As I have stressed elsewhere (Torres de Assumpção 1983) it is necessary not only to make censuses of the primate populations in the remnant forests and obtain information on habitat preference, seasonal stresses and the competition between species, but also to keep monitoring small populations, as they may not be stable and may require active management.

I.4 - Interaction between primates and environment

One of the most obvious aspects of the interaction between primates and environment is their predation on animals and plants. Other less evident interactions include the primates' role as pollinators, seed dispersers, modifiers of forest structure, germination accellerators, etc.. Some of these aspects will now be considered, in the light of the data obtained at B.R.

I.4.1 - DIET

- Methods

I took notes on every instance in which a primate seemed to be searching for prey or collecting a food item. I tried to obtain a sample of every item that the primates were seen to ingest. This was often possible for food items of plant origin, but rarely so for animal prey, which was either non-identifiable from a distance, or unobtainable.

Samples were obtained either from small individuals of the same plant species or from the ground (items dropped by wind or animals). I tried to get items which had the same size and colour as those chosen by the primates. Samples were kept in plastic bags and in the shade until taken to the ranch (on the same day). They were then dried to constant weight in an electric drier (5 to 10 lamps of 100 W). The drying temperature oscillated but rarely reached 60 degrees Celsius. The fresh and dry weights of samples were measured with 200 g spring scales (precision: 1g); this yielded a rough estimate of the water content of the samples. Some samples were put into alcohol before being dried - for these the water content is unknown. The dry samples were kept in plastic bags until taken to the laboratory several months later. In the lab they were ground and dried again (residual water was around 10% of dry sample weight). Because of the restricted mass of the samples (rarely above 8g dry weight), only some tests could be performed. The samples were screened for alkaloids, and then analysed for their lipid, protein and carbohydrate content. There was not enough material for fibre analysis. The screening for alkaloids was done in the following way: the dry tissue was extracted twice with 96 % ethanol, the second extraction being at 50 degrees Celsius. Aliquots of the extracts were chromatographed on silicagel plates with 4:2:1 butanol-water-acetic acid; one set of aliquots was sprayed with Dragendorff reagent, and the second one with iodo platinate. A positive result was accepted only if a positive reaction was obtained in both sets. At least one repetition was done for the "positive" samples. However, this method is not completely satisfactory. Negative results are reliable, but the

indicators used may give positive results even in the absence of alkaloids, if, for instance, substances like flavonoids are present in the sample. (P.Waterman, pers.commun.). In the present case, the samples that produced positive results are likely to contain alkaloids, because they belong to plant families well known as alkaloid producers (Raffauf 1970).

After alkaloid testing, the samples were reconstituted (by mixing extract and residue again) for the next batch of tests (lipid, protein and carbohydrate content) to be executed. Lipids were extracted with hexane and then weighed; after saponification the fatty acids were identified by their retention time in a gas chromatograph. The amount of protein was determined by a variation of the micro-Kjeldahl method, as described in Bataglia et al. (1978); what is in fact measured is the amount of N in the sample, the mass of protein being obtained by multiplying the mass of N by an "universal" factor (6.25). The amount of short chained and long chained carbohydrates was assessed by colorimetry (Dubois et al., 1956) after their separation by the method used by Teixeira et al (1979). The "long chained" carbohydrates do not include cellulose or lignin, only storage carbohydrates. Because the samples were much handled before this last set of tests, a certain amount of the constituents has probably been lost, particularly in the case of lipids, that tend to stick to the containers.

The quantification of feeding behaviour was done in the following way: a score was given for a particular item when its ingestion was first observed. If feeding on the same item continued for an extended period, a second score would be given only every 10 minutes. In most cases, after 10 minutes either the animal had gone out of sight, or the feeding bout on that particular item was over. If within the first 10-min period a different item was seen to be ingested (e.g. another plant species), the new item would get a score. Thus, a given 10-min interval may have provided scores for more than one food item.
This procedure aimed at not biasing the tally towards items whose collection was relatively easy to observe. Intervals of less than 10-min were not used in the analyses because the interval with which notes were taken at the site varied and were often longer than five minutes (see I.3.1.4).

- Results

Appendix I.2 lists the items seen to be eaten by primates at B.R., and also indicates the number of 10-min intervals when each item was seen to be eaten. Table I.15 summarizes the information of App.I.2. Such values provide a crude estimate of the relative importance of each item. However, if an item is eaten more frequently only because it is available for a longer period, the total score is not very indicative. A slightly better index is

TABLE I.15
NUMBER OF 10-MIN INTERVALS WHEN EACH FOOD CATEGORY
WAS SEEN TO BE EATEN BY EACH PRIMATE SPECIES
(percentages between brackets)

	LEAVES		FLOWERS		FRUIT (**)		SEEDS	NECTAR	TRUNK EXUDATES
	young (*)	mature	not open	open	mature, maturing	very immature			
CEBUS n=194			4 (2.1)	6 (3.1)	74 (38.2)		60 (30.9)	50 (25.8)	
ALOUATTA n= 42	3 (7.1)	21 (50.0)	2 (4.8)	1 (2.4)	6 (14.3)	9 (21.4)			
BRACHYTELES n=42	7 (16.7)	1 (2.4)			31 (73.8)		1 (2.4)	2 (4.8)	
CALLICEBUS n=1					1				
CALLITHRIX n=9									9

(*) - including shoots
(**) - "Fruit" includes pulp or aril. Seeds may be ingested but are not masticated.Corn (occasionally supplied by hunters) has been excluded.

obtained by dividing the number of 10-min intervals by the number of months during which the item was available. This index ("P" in Appendix I.2) cannot be compared across primate species, because of the differences in observation time quoted at the top of the table. Index "P" is very crude because the phenological information is coarse and the scores are few. Also, it does not take into account the abundance of each item during the period when available. To accept "P" one has to assume that primates would find and eat any suitable item that was available, independent of its abundance, and that the probability of the item ingestion being observed is strictly proportional to the frequency with which the item was eaten. In spite of these difficulties, the index helps to identify the items that are relatively important in the diet of a given species. For example, it is clear that the nectar and the seeds of Mabea fistulifera, and also the aril of Copaifera langsdorfii, are important items of Cebus diet.

Tables I.16 and I.17 present the results of the chemical analyses for some of the food items. The remaining items were either not sampled or the sample was insufficient for chemical analyses.

- Discussion

CALLICEBUS

Only one feeding instance was observed for Callicebus (on fruits of Cryptocarya moschata, day phase III). It is probable that Callicebus at B.R. feed extensively on this item during the months when it is available, since all three species of Callicebus seem to be relatively specialized frugivores, with a few items (generally

TABLE I.16

CHEMICAL CONSTITUENTS OF SOME ITEMS EATEN BY B.R. PRIMATES
(ALL VALUES ROUNDED)

ITEM (Number and description as in Appendix I.2)	% WATER IN THE FRESH SAMPLE	PERCENTAGE OF THE DRY WEIGHT			
		LIPIDS	PROTEINS	CARBO-HYDRATES (short+long chain)	NOT ANALYSED
1. Cryptocarya	92	8.6	8.3	69.2 (55.7 + 13.5)	13.9
2. Eugenia	(not det. >90 ?)	12.5	15.7	39.5 (31.8 + 7.7)	32.3
3A. Esenbeckia (as eaten by Brachyteles)	(not det., >80 ?)	2.2+	15.8	25.3 (7.8 + 17.5)	56.7
3B. Esenbeckia (as eaten by Cebus)	(not det.)	2.7+	15.0	32.6 (17.8 + 14.8)	49.7
4. Copaifera	66	1.7	7.7	31.4 (28.2 + 3.2)	59.2
5. Psychotria	82	1.5	5.8	49.4 (41.8 + 7.6)	43.3
7A. Mabea (immat.seed)	86	9.4	9.0	35.7 (20.0 + 15.7)	46.0
7B. Mabea (mature seed)	42	29.6	18.0	17.7 (9.0 + 8.7)	34.7
10. Ocotea	(Field:73; residual not det.)	22.8	15.6	10.9 (2.7 + 8.2)	50.6
12.Philodendr. (flower)	72+	19.3+	15.9	40.8 (16.4 + 24.4)	24.0
13.Philodendr. (leaf)	64	15.0	20.0	21.2 (8.1 + 13.1)	43.8
15. Mouriri	79	28.8	19.7	10.3 (4.1 + 6.2)	41.1
18. Miconia	(not det. >80 ?)	3.7	13.4	22.9 (4.4 + 18.5)	60.0

19. Xylopia	(Field:57; residual not det.)	23.5+	10.5	24.9 (8.1 + 16.8)	41.1
20. Qualea	(not det.)	2.7	11.0	18.5 (11.7 + 6.8)	67.9
22. Duguetia	80	2.1	20.4	20.9 (4.4 + 16.5)	56.6
24. Aspidosp.	82	5.8	9.7	33.1 (16.2 + 16.9)	51.3
25. Astronium	(not det.: liquid gum)	4.7	8.8	36.9 (27.6 + 9.3)	49.7
27. Zea (**)	11+	4.3	8.3	75.4 (mostly long chained C.H.)	12.0
*29. Gonatogyne	(not det.)	33.3	6.8	14.7 (2.1 + 12.6)	45.2
32. Inga	78	1.2	19.2	36.6 (15.6 + 21.0)	43.1
*35. Myrcia	(not det. >80 ?)	17.5	7.4	~18.6 (unreliable)	~56.5
49. Eugenia	24	1.6	9.2	55.6 (4.4 + 51.2)	33.5
51. Zollernia	82	3.0	16.9	43.7 (19.7 + 24.0)	36.4
59. Atta	41	50.4	24.7	12.2 (3.0 + 9.2)	12.6

* - These nutrients may not be utilized by the primates; these values are for a sample including seeds, but these may be defecated.

** - data from Gallo et al. (1976)

TABLE I.17

FATTY ACIDS IN THE DIET OF B.R. PRIMATES

expressed as % of lipidic fraction weight; those below 15% omitted.

The figures within brackets indicate the number of carbons and the number of double bonds in the f.a. molecule. The cases where a single f.a. constitutes at least 10% of the item's dry weight are indicated by asterisks.

ITEM (Number and description as in Append.I.2	PALMITIC (16:0)	ESTEARIC (18:0)	OLEIC (18.1)	LINOLEIC (18:2)	LINOLENIC (18:3)	Other f.a.
1. Cryptoc.	24.4			17.7		15.2 (18:3)
2. Eugenia	21.6			24.3		
3A. Esenbec.	27.0			34.5		
3B. "	27.8			29.9		
4. Copaife.						62.9 (20:3)
5. Psychot.			28.9	38.3		
7A. Mabea	19.2					
7B. "				21.4	57.8 [* 17%]	
10. Ocotea	32.2		34.7	21.0		
12. Philo-fl	22.7		53.1 [* 10%]	16.4		
13. Philo-lv						19.2 (18:3)
15. Mouriri			27.4	53.0 [* 15%]		
18. Miconia	14.8		30.5	34.8		
19. Xylopia	18.2		41.7	33.9		
20. Qualea	30.2		41.5			
22. Duguetia	16.5		27.8	41.5		
24. Aspidos.	31.1			27.9		16.4 (20:2)
25. Astroni.			75.0			
27. Zea	16.3		35.5	46.7		
29. Gonatog.	23.8		30.4	30.3		
32. Inga	23.8		15.7			
35. Myrcia	21.1	22.6	26.3			
49. Eugenia	24.5		24.0	29.3		
51. Zollern.	18.4		16.8	35.0	15.9	
59. Atta	25.3		57.7 [* 29%]			

soft-fleshed fruit) constituting the bulk of their diet in a given season.

The C.moloch studied by Janson spent almost 50% of their feeding time eating the fruit of two species of Moraceae (Kinzey 1981). The better known C.torquatus showed a very similar pattern in two of the three seasons sampled (Kinzey 1981). The C.personatus at Sooretama (Brazil) were observed to spend 41% of the feeding time eating fruits from a single species (Kinzey and Becker, in press). It is not unlikely that this may be happening at B.R. Although I was not able to observe Callicebus for an adequate amount of time, it seems that these animals spend a large proportion of their time resting, or at least not moving (they were immobile - and tended to remain so - on six of the 11 occasions when I spotted them before they saw me). I did not observe them to travel by jumping across gaps or running for long periods. Therefore I suspect that, while available, the abundant and rich Cryptocarya fruits (70% carbohydrates) provide most or all the energy that Callicebus require. Nevertheless, this item (as most fruits) is not rich in protein, and the Callicebus at B.R. are likely to have to complement their diet with flowers, leaves or insects, as do the other species in the genus. The non-frugivorous part of their diet is known to vary with the species (Kinzey 1981, p.252) and with season (Kimura dos Reis, pers.comm.).

CALLITHRIX

Only two feeding instances were observed for Callithrix (different days; one bout during phases II and III, and the other during phases IX and X). On both occasions the marmosets fed on exudates from a

particular individual of Astronium graveolens. The marmosets scrape the trunk with their lower teeth and lick the lesion. The shape and size of some lesions indicated they were repetitively used by the marmosets. The aspect of the trunk is shown in Fig.I.22 ; the trunk is by no means covered with lesions, as has been described for other trees whose exudates are ingested by marmosets (e.g. Tapirira guyanensis, see Coimbra Filho and Mittermeier 1978, Rizzini & Coimbra Filho 1981).

A.graveolens is a common tree at B.R. (perhaps more frequent in forest type "A"), and it may reach a big size (25 m high, 40 cm d.b.h.) but I did not observe marmoset-drilled holes in other individuals except the one mentioned (which was not fully grown). This resource may be underused, or perhaps young trees are preferred.

This is the first time that C.j.aurita has been observed to feed on exudates, but this behaviour is known for several other Callithrix forms in the wild: C.humeralifer (Rylands 1982), C.j.penicillata (Rylands 1982, Ratter 1980, Fonseca et al. 1980, Lacher et al. 1981), C.j.jacchus (Stevenson & Rylands in press, Maier et al. 1982). It is interesting to note that some plant families are more used by the marmosets than others. Out of the 61 plant species whose exudates are known to be ingested by Callithrix, 31% are Leguminosae and 15% are Anacardiaceae. These high frequencies are partly due to the local abundance of the families (for example the family Vochysiaceae, relatively abundant in the central Brazilian plant formation, is known to be used only by the local form of Callithrix (C.j.penicillata)); Fonseca et al. (1980) stressed that C.j.penicillata ate exudates from Vochysiaceae more

than from any other plant family. Nevertheless, availability is not the only variable involved. These plant families probably produce more suitable exudates for marmoset feeding, either because of their nutritive value or their lack of secondary compounds. In some cases the nutritive value of the ingested exudates is clear (e.g. that of Anacardium occidentale is 84% carbohydrate (Coimbra Filho & Mittermeier 1976)), but this is not always so (e.g. Hanchornia speciosa, see Rizzini & Coimbra Filho 1981).

A.graveolens is a good energy source (carbohydrates) and has no alkaloids. Nevertheless, the exudate has a strong camphor-like smell, which often indicates terpenoid presence. It becomes resin-like (hard and brittle) with time. However, because it can be dissolved in water but not in pure alcohol, it is more appropriately classified as a gum.

Callithrix are known to eat fruit, flowers, exudates, and to capture and eat animal prey (arthropods, birds, lizards) (Hershkovitz 1977, C.Alonso, in prep., Fonseca et al. 1980). In the wild, C.j.jacchus were observed to spend a large proportion of their time foraging for animal prey among dry leaves, in vine tangles and in trunks (C.Alonso, in prep), but at B.R. I did not observe C.j.aurita foraging in this way, possibly due to their alertness whenever I approached.

BRACHYTELES

The Brachyteles at B.R. were seen to consume fruits, nectar, immature seeds, shoots, young and mature leaves. The nature of these items agrees with the diet type suggested by the examination of the contents of a few stomachs (Aguirre 1971, Hill 1962). In the

stomachs examined, plant matter predominated, although a few items of animal origin were also found. Aguirre (1971) quoted a personal communication about the ingestion of frogs and Orthoptera by these primates. I did not observe Brachyteles foraging for animal prey at B.R. . Some of the animal matter found in the stomachs examined is probably, as suggested by Hill, a contaminant of the vegetable matter ingested.

Brachyteles were seen to eat young leaves more often than mature ones (the only mature leaves I saw them eating were quite soft liana leaves, probably a Bignoniaceae). Leaves seem to be the major source of protein for Brachyteles. The animals' preference for young leaves may be associated with their higher protein content [C.Hladik (1978) stated that protein constitutes 25-35% of young leaves/buds dry weight, whereas mature leaves contain 10-20. It should be noted, however, that the figures mentioned by Hladik (above) are averages, the individual values varying widely (see Appendix I.3). Unfortunately I was unable to obtain samples from the leaves Brachyteles ate.]

Brachyteles seem to eat fruits for their sugar content. The ones they were seen to eat at B.R. were rich in carbohydrates (average for Brachyteles- selected fruit: 41.3% [n=4 , st.d.= 19.5]; average for fruits examined at B.R.: 35.4% [n=10 , st.d.= 18.2]). They also lick nectar, which (although not analysed for chemical content) is certainly very sugary.

Shoots were ingested mainly during the dry season, and may represent a non-preferred item, eaten more frequently when there is less fruit available.

Although the number of 10-min intervals during which

Brachyteles were seen feeding was small (n=27), their distribution suggests a feeding peak at the middle of the day (Fig. I.23A).

ALOUATTA

Alouatta were seen feeding on leaves (young or old), on flowers (buds mostly), and on fruits (mature or not), but more often they ate leaves than fruits. The Alouatta fusca observed by Silva (1981) at Cantareira (Sao Paulo) also seemed to feed mainly on leaves (70% of 12 feeding observations). At B.R. Alouatta seem to be more folivorous than Brachyteles; their diet is likely to be relatively poor in carbohydrates. A striking feature of the howlers' diet is the importance of the liana component. This may be related to the fact that fast-growing plants tend to contain less secondary compounds than slow-growing ones; the non-deciduous lianas are also probably an important source of water during the dry season.

In 1979 I encountered Alouatta on 38 occasions (average encounter duration: 41 minutes), and I observed them feeding on 14 ten-minute intervals, spread across day phases I,II,V,VIII,IX,X and "XI" (i.e. "after sunset"); in Jan/80 I was able to follow a troop of 11 individuals for almost a whole day (7h10 to 18h05) and I observed bouts of intensive feeding at day phases II,III, VII, VIII, IX and X. During these bouts almost all animals fed, whereas between bouts only one or few did, and only lightly (phases IV,V). Thus, although feeding can be observed at almost any time, it seems to be concentrated in certain periods (Fig.I.23B). Feeding bouts are separated by periods of almost complete immobility, around day phases V and VI. This contrasts with Brachyteles feeding pattern, which is intriguing, since both species have partly overlapping

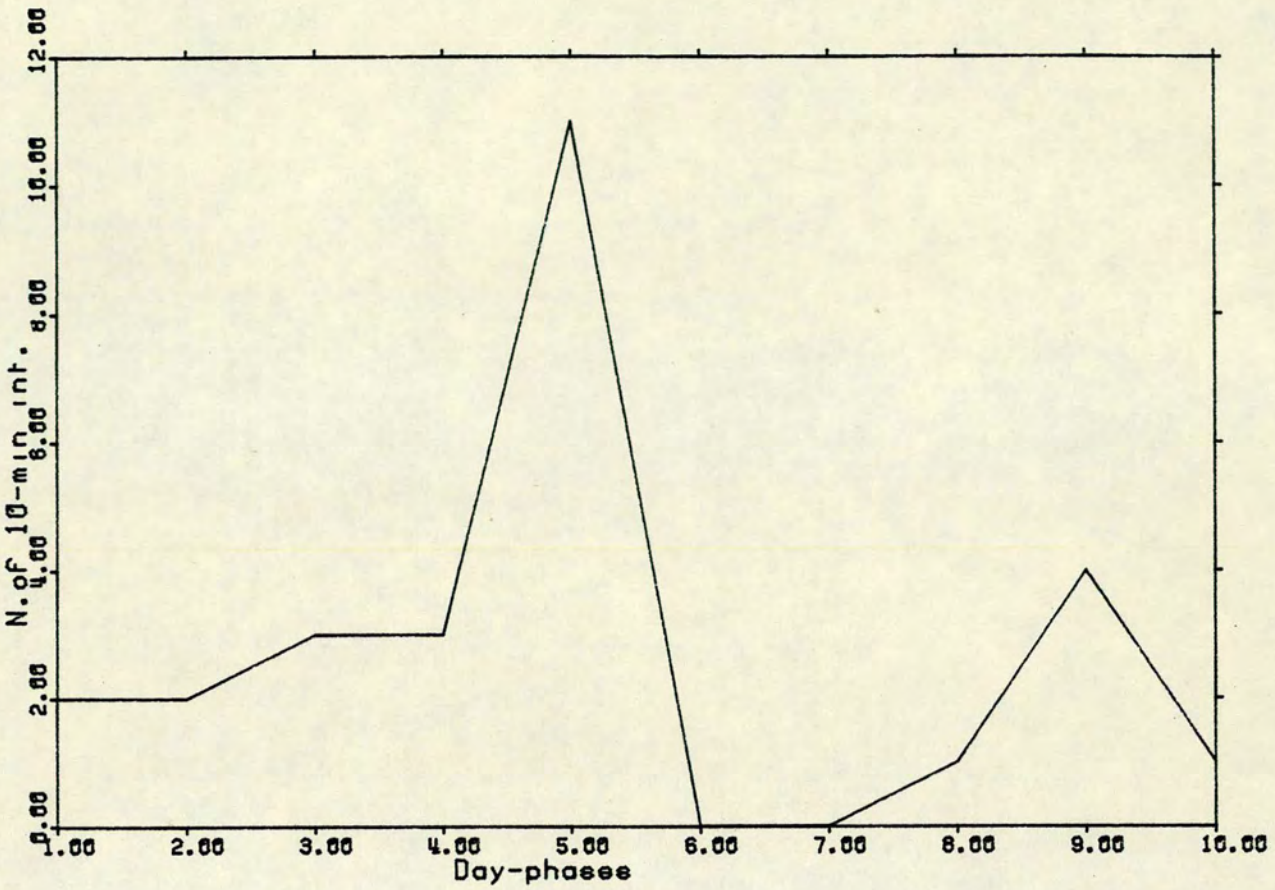
Fig.I.23 - Distribution of feeding across the day.

A- Brachyteles

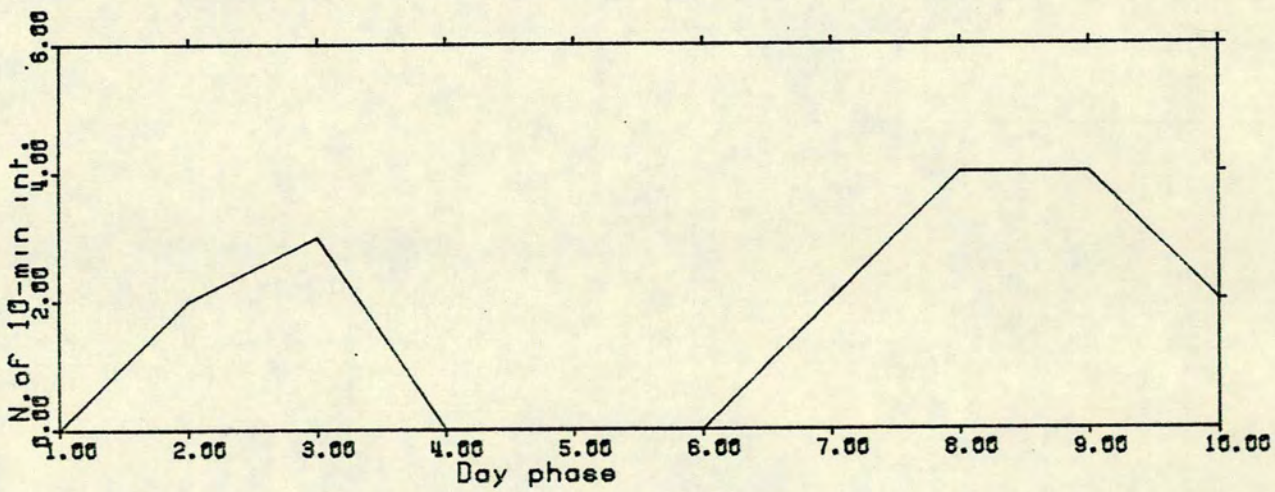
(n=27 ten-min intervals; data collected between Jan. to Dec.1979)

B- Alouatta

(n=14 ten-min intervals; data from a single day in Jan/80; intervals scored only if a minimum of 3 animals fed during that period)



A) BRACHYTELES



B) ALOUATTA

diets. However, conclusions cannot be drawn with such small samples.

CEBUS

Cebus at B.R. were seen to ingest both animal prey and plant parts (arils, pericarps, flowers, seeds, nectar, but apparently no leaves). See Tables I.15 and I.18. The amount of seed in the diet (table I.15) seems higher than in any other Cebus study, and may be due to the fact that dry, dehiscent fruit are more abundant at B.R. than in other sites where C.apella has been studied. The proportion of animal prey in their diet averaged 31% during 1979 (Table I.18), but if only the months where n>30 are considered, the average is 28.5% (st.d=10.5). No comparable figures have been published for C.apella elsewhere, but C.capucinus at Barro Colorado seem to ingest similar proportions of plant and animal matter: 20% animal prey (especially insects), 65% fruit and 15% green material (these figures are proportion of weight eaten rather than % of time spent feeding, from Hladik and Hladik 1969). Hladik et al. (1971) indicated that the diet of C.capucinus at B.C.I. is particularly rich in lipids, partly because of their liking for the fruit of a palm tree (Scheelea zonensis).

The C.apella studied at La Macarena (Izawa 1978, 1979), were also primarily frugivorous and insectivorous and also showed a strong liking for palm fruits.

Struhsaker and Leland (1977) also mentioned the importance of Astrocaryum palm fruit for C.apella. At B.R. there are few palms but, nevertheless, the local Cebus' diet is still very rich in energy (both sugar and lipids - the latter coming mainly from the

TABLE I.18
PROPORTION OF ANIMAL PREY AND PLANT MATTER IN B.R. *CEBUS* DIET

	- Months -											
	J	F	M	A	M	J	J	A	S	O	N	D
ABSOLUTE VALUES:												
Animal prey (*)	0	1	3	7	4	8	20	13	15	6	12	14
Plant matter	5	7	26	17	20	21	25	21	28	8	1	11
Uncertain	0	0	0	2	7	5	6	3	4	1	0	3
TOTAL (n)	5	8	29	26	31	34	51	37	47	15	13	28
PERCENTAGES:												
Animal prey	0	12	10	27	13	24	39	35	32	40	92	50
Plant matter	100	88	90	65	64	62	49	57	60	53	8	39

(*) If peeling of branch/trunk was maintained for several minutes, "animal prey" may have been scored, even if animal items were not actually seen to be ingested.

seeds of Mabea fistulifera).

The ingestion of relatively large amounts of Mabea fistulifera seeds is intriguing. Mabea seed oil is unusually rich in linolenic acid (see Table I.17), which makes this oil very similar to linseed oil. The animals might be forced to eat this item for its energy content because at the end of the dry season there is little else available, but it is relevant to know that the linolenic acid (present in such an unusual amount in Mabea seeds) has been shown to be essential for Cebus nutrition (Fiennes et al. 1973, Sinclair et al. 1974). Cebus kept on a linolenic-acid-free diet develop skin lesions and gnaw themselves to the point that septic wounds are formed and experimental animals have to be put down. Even if further research shows that Cebus are not the only mammals for which this fatty acid is essential, (Rivers and Davidson 1974), the fact that Cebus need it may explain why they put such effort into opening the amazingly hard Mabea fruits to obtain these seeds. (Mabea seeds may have up to 50% dry weight of a strongly scented oil; figure from unpublished tests carried out by ITAL-Campinas, Brazil)

At B.R. (as in many other localities), Cebus raid neighbouring corn plantations. However, the troops that I observed only obtained corn from a hunting hide where it was occasionally placed in large amounts. When corn was available at the hunting hide, Cebus seemed to remain nearby, and were once observed to "defend" this resource against other troops.

Cebus do not only eat items that are well exposed (e.g. fruits), but forage very actively, manipulating clusters of dead leaves, digging into trunks, investigating the inside of branches, hard-shelled fruits, etc.. Several authors (e.g. Izawa 1978 A & B,

Izawa and Mizuno 1978, Struhsaker and Leland 1977) have remarked on how complex and purposeful is Cebus apella feeding behaviour. Detailed descriptions are found in Izawa's papers. Cebus may be found at any height in the trees and, although not often seen to come to the ground at B.R., they do so frequently at other sites (e.g. Ourinhos), and at B.R. they also cross roads to get at the neighbouring forest block. These characteristics (manipulating ability, opportunism and versatility) are certainly linked with C.apella' success in spreading over such a wide geographical range.

Cebus seem to eat mainly during the early morning and late in the afternoon, although they may be seen eating anytime in the day (see Fig.I.24).

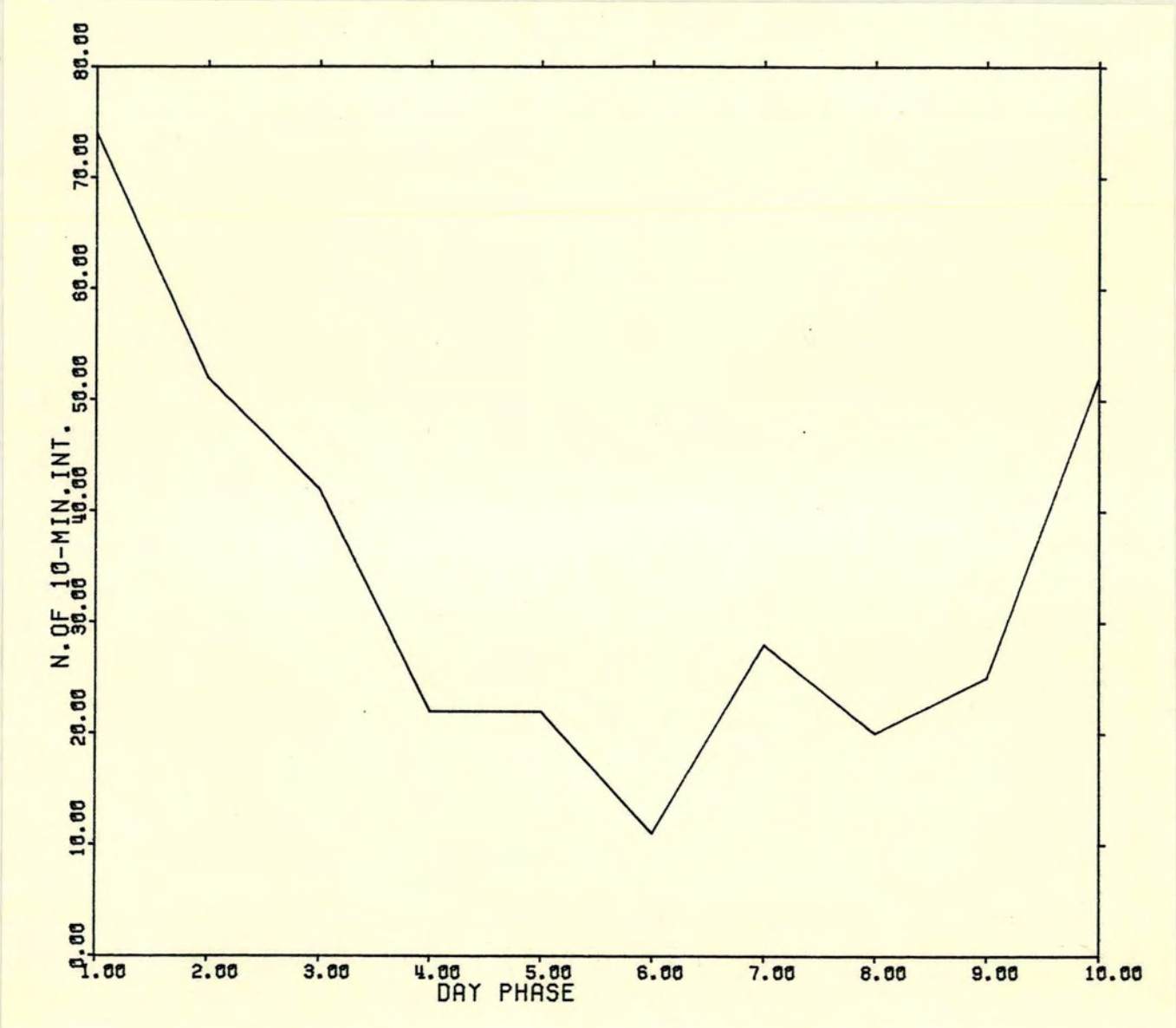
GENERAL

The information obtained on the diet of B.R. primates is restricted and does not allow detailed analyses. For Callicebus and Callithrix it can only be said is that the items seen to be eaten agree with what was expected on the basis of the diets of closely related forms.

Alouatta and Brachyteles diets are roughly similar and partly overlapping. Lianas are important in the diets of both species. Both ingest mostly leaves and fruit, although Brachyteles ingests a larger proportion of energy rich fruits; this links well with their more energetic locomotion - they can travel much faster and over much longer distances than Alouatta. Their diet may also be less burdened by secondary compounds, since they seem to select more immature leaves than Alouatta does.

It is interesting to note the parallel with Milton's (1980A)

Fig I.24 - Cebus feeding across the day. Pool of all data collected during 1979 (n=348)



comparison between Ateles and Alouatta diets. Ateles, like Brachyteles at B.R., are more frugivorous than Alouatta; their diet is rich in carbohydrates but not in proteins, whereas the diet of the more folivorous Alouatta shows the opposite trend. Milton associated these diets with different digestive strategies. Alouatta ferments refractory plant parts more efficiently than Ateles, and maximizes energy return from leaves. Ateles processes larger amounts of food per unit time and specialize on fruit whose protein content is too low to support howlers. Milton (1980A) suggested that these different strategies help to minimize competition between the two species. The same could be happening at B.R.

Cebus have the most diversified diet of all B.R. primates. Their more extensive list of diet items is partly due to them having been observed for longer, but surely Cebus exploit more niches than the other species do.

Seasonal stresses from differences in food availability must exist, but my data are too coarse to allow more than speculation. Species which exploit fleshy fruits (e.g. Brachyteles and Callicebus), are more likely to be stressed during the dry season, when most of the available fruit are dry dehiscent structures (see Table I.5 for the fruits available at each month). These primate species may be reducing their activity level during the dry season; this would explain why there is such a drop in the observation time for these species during the dry season in spite of my effort in looking for them being constant (data in Tables I.6 and I.11). Although the drop in Brachyteles observation time could also be due to their staying outside the intensive study area, that should not be the case with the less mobile and possibly territorial

Callicebus. Cebus seem to be adopting the reverse strategy, i.e., increasing foraging time and distance travelled per day during the dry season. Presumably, during this period of scarcity, only species with a varied diet can find enough suitable food to justify an increase in foraging effort.

The data obtained during this study do not allow conclusions as to whether there is competition for food among the primate species at B.R. Because the forest is low and the canopy does not have several layers, the classical spatial isolation through the use of different strata is unlikely to hold for this site. Brachyteles, Alouatta, Cebus and Callicebus all seem to use the canopy either exclusively or preferentially. Callithrix, although often seen near the ground (see I.3.5), also use the canopy. There is no indication that a primate species excludes others from a given area, although some avoidance may occur (see I.3.8). If there is competition between species, it is more likely to be minimized by temporal rather than by spatial means.

THE IMPORTANCE OF FOREST TYPE B

The fact that some important food items can only be found in forest type B (e.g. those from Mabea fistulifera, Duguetia lanceolata and Eugenia sp 7517) illustrates how relatively small areas can be crucially important for the animal population. The removal of forest B would not necessarily mean the disappearance of the primates, but it would produce serious stress. The removal of small important sub-habitats like this may explain why in some other (similar) remnant forests the primate population is less diverse.

I.4.2 - PRIMATES AS POLLINATORS

A number of instances of primates acting as potential pollinators has been recently reported. Sussman (1979) mentioned cases in which prosimians were involved, and Oppenheimer (1968,1977) provided the first description involving a monkey: Cebus capucinus as a possible pollinator of Ochroma pyramidale (Bombacaceae) at Barro Colorado, Panama. Mori et al. (1978) observed Cebus apella and Saimiri foraging on nectar from flowers of Eperua falcata (Leguminosae) in Suriname. Prance (1980) indicated that Cebus apella might pollinate Combretum lanceolatum (Combretaceae) at Mato Grosso, Brazil. At Cosha Cashu, Peru, Janson et al. (1981) observed at least seven primate species visiting the flowers of Combretum fruticosum (Combretaceae) and at least five at the flowers of Quararibea cordata (Bombacaceae). At Barreiro Rico both Cebus apella and Brachyteles arachnoides seemed to pollinate Mabea fistulifera (Euphorbiaceae). Details are found in Torres de Assumpção (1981), included here as Appendix I.5.

Even if the primates are efficient pollinators in the cases mentioned above, it is not certain that there has been co-evolution between them and the plants they pollinate. The cases reported include more than one type of flower; the primates are not restricted to a "primate-as-pollinator" syndrome. Janson et al. 1981 suggested that there is a "non-flying mammal" floral syndrome (a tough, partially fused perianth in the form of a shallow cup; long exserted stamens; sessile, fasciculate inflorescences; upright orientation of the flowers; tendency to produce large fruits; visual conspicuousness through flower production during periods of leaflessness) but this seems too broad a generalization, since the

size and morphology of non-flying mammals can be so varied. Reliable, co-evolved pollinators (just as co-evolved seed dispersers), are expected to get most of their nutritional requirements from the pollinated plant, on which they would be strongly dependent (Snow 1970,1981; Howe 1977). The monkeys' feeding habits (particularly in the case of Cebus) do not fit this description; these animals seem too opportunistic to be reliable pollinating agents. Van der Pijl (1969, p.46) has pointed out that monkeys are "latecomers" (in the sense of coevolution with plants) and that they merely take advantage of ecological opportunities, and that they are mostly destructive. Primates may be important as pollinators only when the coevolved agents are absent, either flying ones, as suggested by Sussman (1979) or non-flying ones, as suggested by Janson et al. (1981).

I.4.3 - PRIMATES AS SEED DISPERSERS

At B.R. primates were observed to remove seeds from fruits, and either discard or ingest them. Examples of the first case involve the removal of the alate seeds of several bignoniaceous lianas by Cebus. The animals probably open the pods in search for animal prey; this activity is likely to lower the plant's reproductive potential, because the seeds may be removed while still immature. If the seeds are ingested, they may be masticated or not. In the first case the animals are merely exploiting the plant, but in the second case they may be acting as seed dispersers, by defecating intact seeds away from the parent tree (endozoochory). Examples of endozoochory are marked with "S" in Appendix I.2. In

most cases it seems clear that both plant and animal benefit from the arrangement (see for example the nutritive value of the pulp of Eugenia sp. 7517 and Nectandra aff. spixiana 7528). However, the relationship animal/plant is not clear in all cases. For example, the seeds of Mouriri sp 7521 are eaten by Cebus both before and after maturation; before maturation the pericarp of immature fruits is discarded, but the seeds are masticated and ingested. When the fruits mature, the animals swallow the seeds whole, and also the sweet mucilage that covers them; such mature seeds can be found intact in Cebus faeces. Because Mouriri produces initially many fruits which are later shed (in fact many of these fruits do not develop seeds), Cebus predation at the early stages may not affect the plants' reproduction.

In one particular case (ingestion of Gonatogyne brasiliensis seeds by Cebus) it was difficult to know what benefit the monkey might be getting. The fruit of this species is dry, hard, small; considerable effort and accurate manipulation are required to open such fruit and get the seeds. However, the animals do not seem to absorb the seeds, which may be found intact in Cebus faeces. Perhaps some of the seeds are masticated and absorbed, in which case the animals would be getting an energy-rich food (high proportion of lipids).

Examples of seed predation at B.R. are indicated with the letter "D" in Appendix I.2, and in most cases the seeds are consumed while still immature.

I.4.4 - PRIMATES AS ACCEL͡ERATORS OF SEED GERMINATION

Hladik &. Hladik (1969) have shown that seeds may have a higher germination rate and a shorter germination time after having passed through primate guts. Provided that these properties give the ingested seeds a better chance (e.g. when competing for light), seed ingestion by the monkeys may be beneficial to the plant.

To examine whether at B.R. Cebus were acting as germination accel͡erators, I obtained seeds from Cebus faeces and placed them on damp cotton wool, where they were kept (in the shade) for one month; controls of non ingested seeds underwent the same process. This was done with seeds from Miconia sp 7552, Eugenia sp 7517, Faramea sp 7544, Mouriri sp 7521, Nectandra aff. spixiana 7528 and Myrcia (?)formosiana. I did not test seeds ingested by the other primate species.

With the exception of one sample, none of the seeds germinated - neither the controls nor the ingested ones - within the one-month period. The exception was a sample of seeds from (almost certainly) Myrcia formosiana, which germinated the day after they were washed. However, the identification was not firm in this case, and no controls could be obtained.

The germination failure observed may be due, at least in some cases, to the plant's adaptation to a seasonal environment; germination might be delayed if seeds are produced in unsuitable months. A longer test period might be more revealing, but the (restricted) evidence so far does not indicate Cebus as a germination accel͡eration agent.

I.4.5 - THE STRATEGIES OF SOME FOOD-PRODUCING PLANTS

Some plants were particularly important for the primates' diet; it is relevant to examine in more detail their interaction with the primates.

1. Fruits of Cryptocarya moschata (Lauraceae)

This item is eaten by at least four of B.R. primate species, and it is available in large amounts for at least a quarter of the year. It may therefore be a major source of energy for the primates. This tree species is common in the forest (both in forest types "A" and "B"). From the plants' point of view, the production of energy-rich fruits should be compensated somehow, possibly by efficient seed dispersion. Snow (1981,1982) indicated that the South American Lauraceae is a family in which there has apparently been coevolution with seed-dispersing birds. According to Snow, the pericarps of several Lauraceae, shaped as a thin layer around a large-sized seed, are nutritious enough to reward specialized frugivores for the ingestion of the whole fruit, including its big and (for the frugivore) useless seed. Snow considered lipid-rich fruit to be characteristic of this co-evolution. Howe & Estabrook (1977) suggested that the most suitable strategy for this type of plant is to produce relatively few fruits per unit time, just enough to sustain the population of specialized (obligate frugivores) dispersers.

Cryptocarya moschata does not, however, fit the Lauraceae generalization very well. It does have large seeds and a nutritious pericarp, relatively rich in lipids, but it is more sugary than oily (Snow considers sugar as a cheaper investment, typical of fruit produced in large amounts to be dispersed by opportunistic species),

and its fruiting strategy does not fit Howe & Estabrook's model for "specialized" trees. Fruit production is massive and fruits are available for at least three months/year. I was unable to recognize a "specialized-frugivore-syndrome" in this Lauraceae, and I was also unable to find any efficient seed disperser for it. The seeds, round and 1.5 cm in diameter, are too large for most local birds to ingest, and the primates that eat the fruits do not generally swallow the mature seeds (although Brachyteles may ingest small immature ones). Kuhlmann (1975) listed C.moschata seeds as being recovered from A.fusca faeces, but he did not mention whether they were mature. The only other possible dispersers are ground-dwelling mammals (agoutis, peccaries), which might scatter-hoard the seeds. Agoutis are known to bury seeds as a reserve (Van der Pijl 1969, p.40). Very suitable dispersers would be tapirs, but there are presently no tapirs at B.R. The apparently maladapted tendency of these fruit to fall even in the absence of wind makes more sense if one accepts that its dispersal strategy is associated with ground dwellers.

The main point is that, even if this item is extensively used by the primates, they do not seem to benefit the plant in any way, but are merely exploiting it. One wonders whether the situation is stable; young Cryptocarya trees were not observed at B.R.; this could have been due to observational bias towards large fruiting trees, but it may also be an indication that the population of Cryptocarya will not be substituted. If so, this is likely to have a big impact on the future of the primate population.

2. Aril of Copaifera langsdorfii (Leguminosae)

These large trees are common throughout B.R. forest, and occur also in area "C". Copaifera aril, rich in carbohydrate, is a convenient source of food and water during the dry season, and it is extensively used by primates and birds. The seeds of this species can be found in primate faeces, so they have a good chance of being dispersed. Copaifera seedlings were observed in the forest. There is little doubt that this species is using an "opportunistic disperser" strategy - the orange coloured aril contrasts with the black smooth seed, and many fruits are produced at a time. This food seems to be superabundant when it is available, therefore unlikely to promote competition among frugivores.

3. Nectar and seeds of Mabea fistulifera (Euphorbiaceae)

The nectar of M.fistulifera is very sweet and surely an excellent source of energy. Cebus and Brachyteles were seen to ingest this item, and it is likely that other primates also do. The production of nectar is copious and its collection is easy, since there are not flower structures protecting it. Mabea trees can only be found in forest type B, where they are very abundant.

Both Cebus and Brachyteles may be acting as pollinators for this tree species (see Appendix I.5). Cebus, however, also preys on Mabea seeds later in the year. Whether Mabea profits from Cebus presence depends on the balance between the advantages of pollination and the disadvantages of seed predation. In any case, this tree is a very important plant for Cebus survival at B.R.

SUMMARY

I.1 - Characteristics of Southeastern Brazil

1. As a result of its diversified relief, climate and vegetation, southeast Brazil includes a wide range of habitats.
2. Primates occur mostly in the forests of the "tropical Atlantic" morphoclimatic domain, but they can also be found in certain niches within other domains (e.g. gallery forests in the "cerrado" domain).
3. The original landscape of Southeastern Brazil has been much altered by human interference. Forests were reduced to a few patches, threatening the survival of endemic species.
4. The composition and the density of the primate population vary between the remnant forests. In most cases it is not clear whether this is due to the forests reduction and alteration, or whether it reflects the original situation.

I.2 - Characteristics of Barreiro Rico site

1. The forests of Barreiro Rico (part of the "tropical Atlantic" domain) are described on the basis of a 12-month field study. Aspects examined include the local relief, soil, climate, seasonality, fauna and vegetation. The forest is shown not to be homogeneous.
2. The mammals observed at B.R. are listed. For some species data are presented on their spatial distribution and abundance in different seasons.

I.3 - The primate population at Barreiro Rico

1. It is estimated that the primate population of the 115-ha intensive study area consists of: one troop of Brachyteles, four troops of Callicebus, five troops of Cebus, four troops of Callithrix and four (or more) troops of Alouatta. Most of these estimates are based on indirect evidence.
2. No polyspecific associations were observed among B.R. primates. Larger species may displace smaller ones, but interspecific relations are largely neutral.

I.4 - Interaction between primates and environment

1. The items seen to be eaten by the B.R. primates are listed. Some items are common to the diet of more than one species, but these items seemed superabundant when available and did not seem to be a source of competition. Very little data was obtained on the diets of Callithrix and Callicebus; for the other species there was no obvious indication of competition, as the diet of each species seemed to emphasize different types of food.
2. In most cases the action of the primates on the vegetation seemed to be merely exploitative, but in a few instances the monkeys may be aiding the plants' reproduction by dispersing seeds or cross-pollinating flowers.

SECTION II

REAPPRAISAL OF CEBUS APELLA RACES

INTRODUCTION

So far I have avoided naming the race of Cebus apella I was dealing with because there is at present no acceptable arrangement for Cebus apella races.

Anyone interested in identifying any form of Cebus will be confronted with what Hill (1960) called "one of the most vexatious problems in primate taxonomy". The difficulty in classifying the many forms of Cebus is well known and has been commented upon by Cabrera (1917), Cruz Lima (1945) and by many other authors. There are two main reasons for this difficulty: the proneness of Cebus to individual variation and the extreme nomenclatorial confusion which has involved these animals since Linnean times. Hill (1960) provided a good account of Cebus taxonomic history.

The great variation in Cebus may explain, to a certain extent, the complexity of its taxonomy. Not having large samples, the early workers described all the variations as new species, not realizing that the characters were age or sex-linked, or merely individual variations. Some unfortunate revisions (e.g. Elliot 1913, Pusch 1941) complicated the literature even more. Several mistakes were pointed out by Cabrera (1917) and by Hershkovitz (1949, 1955). Hershkovitz's 1949 paper solved some of the earlier confusion. In that paper he confirmed the arrangement of all forms of Cebus into two groups: the "tufted" and the "untufted", depending on whether the animals had elongated frontal hair tufts. At the same time, however, he emphasized that hair tufts might not be present in some forms of the "tufted" group, and therefore the identification of any specimen should be based not only on external characters, but also on cranial and skeletal ones. Hershkovitz assigned only one species

(Cebus apella) to the "tufted" group, and three (C.nigrivittatus, C.capucinus and C.albifrons) to the "untufted" group. Hershkovitz (1949) revised all the "untufted" forms but left the revision of the "tufted" forms to his colleague R.Kellogg. Kellogg died before publishing his revision (P.Napier, pers. comm.), and the only published account of the forms he was prepared to recognize is the one by Hill (1960), based on personal communications from Kellogg.

Hershkovitz's 4-species arrangement was implicitly accepted by Kellogg, and also by Hill (1960). The choice of names was questioned by Tate (1954) but Hershkovitz (1955) dismissed his arguments. Since then Hershkovitz's 4-species arrangement has been widely used (e.g.by Napier and Napier 1967, Jolly 1972, Napier 1976, Moynihan 1976, Chalmers 1979). The fact that this arrangement has been in use for several years does not mean, however, that all problems in Cebus taxonomy have been sorted out.There are controversies at the nomenclatorial level (see Tate 1954 and Hershkovitz 1955, Hershkovitz 1959 and Hill 1955) that are, to my view, not satisfactorily solved. The difficulties are not restricted to the naming of forms - their very recognition is problematical. Looking closely at the presently accepted arrangement, one realizes that at the race level none of the proposed species is satisfactorily studied. For both C.capucinus and C.nigrivittatus Hershkovitz (1949) clearly stated that the proposed arrangement was only tentative (p.347, 348). Even for C.albifrons Hershkovitz's revision cannot be considered final, since the author recognized that the material he had at hand did not cover the entire geographical range of C.albifrons, and that "in the absence of samples of intergrading populations, it is difficult to

assess the characters which unite clans into geographic races" (p.352). Eleven of his thirteen C.albifrons races were defined from the examination of less than 10 individuals each. Such a sample may be inadequate, since Hershkovitz's arrangement is based only on coat colour, and he mentioned a possible alteration of pelage colour with season.

It would be unrealistic to expect that Hershkovitz's preliminary arrangement could accommodate new information in a satisfactory way. Some indications of its inappropriateness are mentioned below:

a. Hernandez-Camacho and Cooper (1976), in a reasonably detailed work on the Colombian primates, were unable to define races for C.capucinus and suggested that at least one race of C.albifrons recognized by Hershkovitz should be synonymized. More importantly, they reported forms intermediate between C.capucinus and C.albifrons from areas where these two species might meet (e.g. middle San Jorge valley, Colombia).

b. Torres de Caballero et al. (1976), using a totally different approach (karyological studies) also indicated the existence of natural hybrids between C.albifrons and C.capucinus. It is relevant to the understanding of the relationship between these two forms that the hybrids mentioned by Torres de Caballero et al. did not come from the area where the two forms might meet (and maybe occasionally produce hybrids), but from an area (Vaupés, Colombia) ascribed only to C.albifrons.

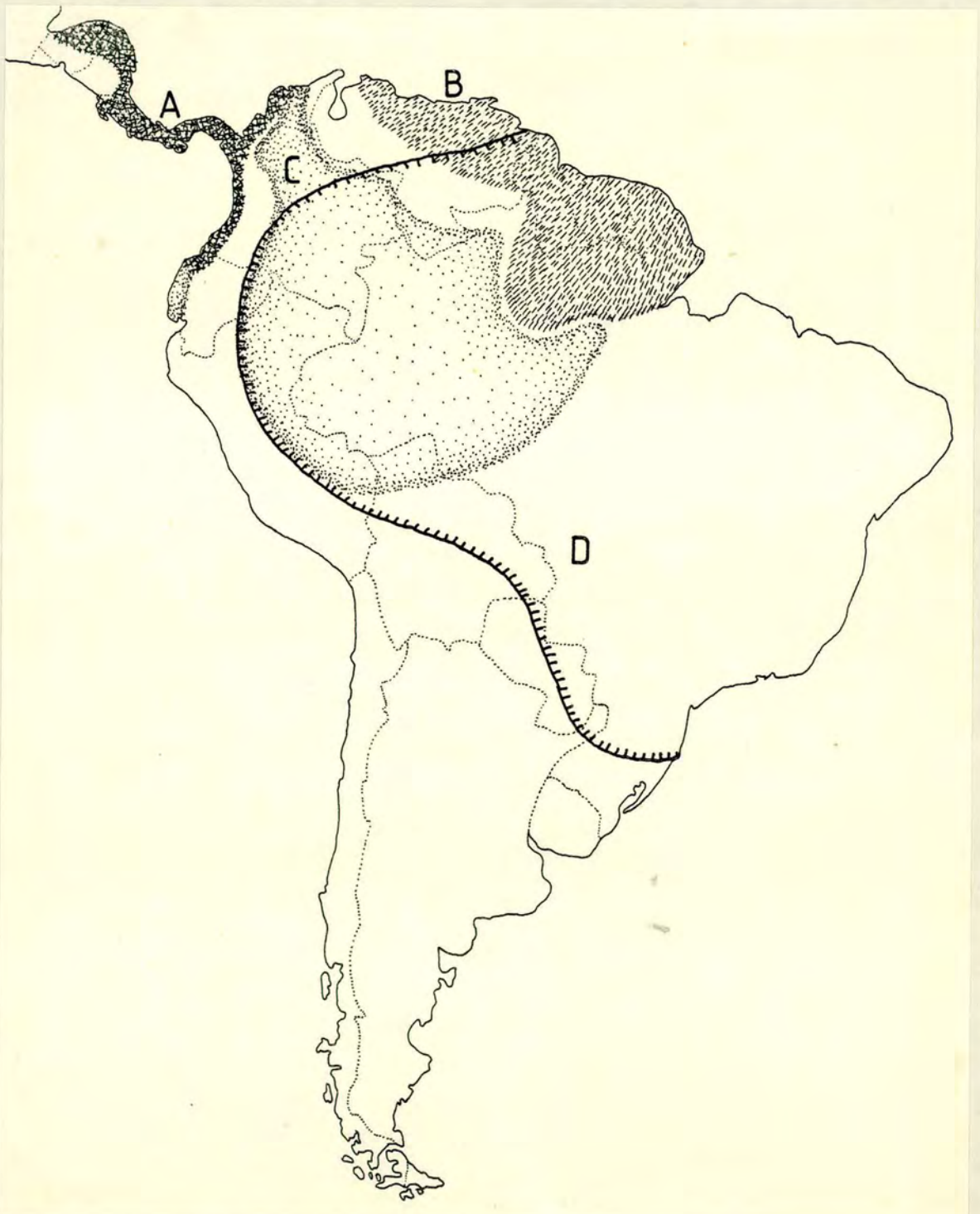
c. The fact that there is no reported sympatry between any of the "untufted" forms might be another indication that these forms are not genetically isolated.

The evidence mentioned above tends to support the idea that the "untufted" forms are not reproductively isolated and there is currently a tendency to lump the species of "untufted" Cebus. Hernandez-Camacho and Cooper (1976) questioned the species status of C.capucinus and C.albifrons, and Mittermeier and Coimbra-Filho (1981) did the same for C.nigrivittatus and C.albifrons. In this last case the authors did not provide the actual data from which their suggestion stems, but their suspicion is declared to be based on morphological characters. The lumping of "untufted" forms into one species is not, however, unanimously accepted. Thorington (1976), for instance, argues that hybridization in a narrow area of contact should not be the basis for lumping of species. Also, it may be argued that the allopatry of the non-tufted forms is due to competitive exclusion (their similar habits preventing them from sharing resources) and not to reproductive isolation (this view seems implicit in Moynihan's (1976) acceptance of four species for Cebus).

Although the information presently available would call for a new study of the whole group, no formal revision has been done. It seems that the taxonomists have been reluctant to deal with (or add to) the earlier confusion.

Even if Cebus species are reorganised in the future, it is unlikely that the reproductive isolation between "tufted" and "untufted" forms will be questioned. The ample sympatry between the "tufted" and the "untufted" forms (Fig II.1) is a strong indication that the "tufted" group is genetically isolated from the "untufted" forms. There are only two reported cases of hybridization between "tufted" and "untufted" forms (Zuckermann (1933) and Bronzini

Fig.II.1 - Very approximate distribution of the four species of Cebus recognized by Hershkovitz 1949. A: C.capucinus, B: C.nigrivittatus, C: C.albifrons, D: C.apella. Based on information from Hershkovitz 1949, Hernandez-Camacho and Cooper 1976, and Napier 1976.



(1949)). The last case may be attributed to the difficulty in naming forms at the time the communication was given, but in the case of Zuckermann (1933) the description of the hybrid's parents leaves no doubt about their identity: they were certainly a "tufted" female and an "untufted" male. No information is given about the hybrid's fertility, and no new cases have been mentioned since (see for instance Gray 1954, 1972 and Chiarelli 1961), in spite of the fact that Cebus albifrons and Cebus apella are commonly kept in zoos and laboratories.

Since the "tufted" group seems to be genetically isolated from the "untufted" one, its morphological variation can be studied independently from all other forms. Yet, the interpretation of the general speciation sequence clearly requires the understanding of the relationships between all forms, "tufted" and "untufted" alike.

As mentioned before, Kellogg's long-waited revision of the tufted Cebus was never published. The previous one, by Pusch (1941), is considered unsatisfactory by Hershkovitz (1949) and has little in common with Kellogg's arrangement and naming. It is true that Pusch's revision is confused. For instance, he mentions C.albifrons from southeastern Brazil, thus placing a light coloured "non tufted" Cebus in an area where only dark "tufted" Cebus occur.

Hill's (1960) account of Kellogg's conclusions has several drawbacks:

a. It is not the real revision but a summary of Kellogg's conclusions mixed with Hill's own observations. The details of Kellogg's original research are not given. The number of specimens examined and the methods used are not specified. Hill's account may even not be a perfect reflection of Kellogg's conclusions, since it

contains several of Hill's own interpretations.

b. it does not indicate the full variability of each race, nor describe the intergrading forms (although Hill acknowledged their existence (p.458)). As a result, specimens with unknown origin frequently cannot be ascribed to any of the described races, and even material with known origin may not fit the description of that area's race.

c. The distribution of Cebus apella races as given by Hill also involves several inconsistencies. For instance, he places two different races (C.a.juruanus and C.a.peruanus) on the banks of R.Juruá, mentioning the locality Igarapé Grande as being inhabited by both races (p.474,475). Sympatric forms can be either 1) variations within the same population, in which case they should not be called races; or 2) genetically, behaviourally or ecologically isolated, in which case they should be considered different species. The same problem involves the locality Chapada, which Hill indicated as being inhabited both by C.a.cay and by C.a.pallidus (p.479,477). Similarly, Colatina is said to be inhabited both by C.a.robustus and by C.a.xanthosternos. These inconsistencies do not show in Hill's distribution map because the map does not conform to the text.

In spite of all these difficulties, Hill's arrangement has been used by researchers because it is the latest summary of the subject. When problems arise, a compromise is made in which some of the forms are accepted and some are discarded (e.g. frontatus in Kinzey 1980, juruanus in Mittermeier & Coimbra Filho 1981) without the reasons for this being clearly stated. Such conclusions cannot be accepted without re-examination of the relevant material.

It is clear that a thorough revision of the group is needed.

All forms should be examined, for, as Vanzolini (1970, p.13) stated, a differentiation pattern can only be understood as a whole. Quantitative characters should be used in addition to qualitative ones, for they are less affected by subjective interpretation. Large samples of all age-sex classes are required to allow the assessment of the intra-population variation. Such a revision is an ambitious task requiring a very large sample and the re-examination of all available types. In this study I did not intend to do a full revision of the species, but to use the abundant material available at the most accessible museums to

- make a new assessment of the "tufted" Cebus morphological variability,
- define the geographical pattern of morphological differentiation by comparing the variability within and between localities,
- use this geographical pattern to investigate the evolutionary sequence of the whole group.

METHODS

The method basically consists of examining various morphological characters in specimens from as many localities as possible and the detection of areas where the characters are stable and areas where character transition or disruption occur. In practice, it involves various steps:

A. examination of a series of morphological characters in as large a number of specimens as possible,

B. mapping of the localities where the examined specimens were collected,

C. a decision as to whether there is only one species involved,

D. pooling of the information yielded by neighbouring localities, whenever necessary and possible,

E. analysis of the characters within the large samples,

F. analysis of the characters between localities.

Each of these steps will be described. The results obtained for each step will be presented in this section and not under "Results", since they are necessary preliminaries to the execution of the steps that follow.

A. EXAMINATION OF MORPHOLOGICAL CHARACTERS IN THE LARGEST POSSIBLE NUMBER OF SPECIMENS

In a preliminary phase all C.apella specimens of the Museu de Zoologia da Universidade de São Paulo (MZUSP) were examined (circa 400 specimens). In the other museums mainly adult specimens were examined. This was done because the time to be spent in the other museums had to be kept at a minimum and immature animals seemed to provide less useful information.

My final sample includes circa 750 specimens (either skins, skulls or skins+skulls). 717 of these specimens had their characters recorded on individual checksheets; the remaining ones were only superficially examined due to limitation in the time to be spent in the museums. Appendix II.2 lists the examined specimens.

The selection of characters was restricted by the kind of material available. As in most mammal taxonomic work, this study is based on pelage colour and skull measurements.

For every specimen I collected the following information:

GENERAL

Specimen's number, sex, collector, collecting date, collecting locality, previous identifications.

SKULL

E1 - presence or absence of sagittal crest. If the crest was only incipient or particularly pronounced, this was also registered. (The sagittal crest is indicated by treble arrows in Fig. II.2)

F1 - age category. This assessment was based on tooth eruption and tooth wear. Details are given in section E.

G1 - skull length (see measurement 1 in Fig. II.2)

H1 - condylo-basal length, measured preferentially on the left side (see measurement 2 in Fig. II.2)

I1 - maximum cranial breadth at parietal bones (see measurement 3 in Fig. II.2)

J1 - zygomatic breadth (see measurement 4 in Fig. II.2)

K1 - orbital breadth (see measurement 5 in Fig. II.2)

L1 - coronoidal height, measured preferentially on the left side (see measurement 6 in Fig. II.2)

M1 - grade of vomer wing pneumatization, according to the scale defined by Della Serra (1950). Some of the skulls mentioned by Della Serra in his original work (skull DZ5918 for grade 1/1, DZ 6013 for grade 2/2 and DZ 5117 for grade 3/1) were used as references during the first assessments. (Vomer wings are shown by double arrows in fig. II.2.)

N1 - length of largest upper canine. If the tip was missing or if the canine was not fully erupted, no measurement was taken (see measurement 7 in Fig. II.2)

O1 - state of spheno-occipital suture: "open", "closed" or

SYMBOL INDEX

* E1 - presence/absence sagittal crest

** F1 - age category

* G1 - skull length

* H1 - condylo-basal length

* I1 - cranial breadth at parietal bones

* J1 - zygomatic breadth

* K1 - orbital breadth

* L1 - coronoidal height

* M1 - grade of vomer wing pneumatization

* N1 - length of largest upper canine

* O1 - state of spheno-occipital suture

A3 - limb colour

B3 - tail colour

C3 - flanks colour

D3 - back colour

E3 - cap colour

F3 - cap shape

A2 - head+body+tail length

C2 - tail length

D2 - foot length

F3 - ear length

G17- specimen's weight

* - see Fig.II.2

** - see Table II.3

"closing". (The spheno-occipital suture is shown by a single arrow in Fig. II.2)

Nearly all the measurements mentioned above were taken with Alpa (mod.1150) calipers, except for the specimens housed at the British Museum, which were measured with Helios calipers. Both calipers had 0.05mm divisions, but the values were read to the nearest 0.1mm.

BODY MEASUREMENTS

These include the standard measurements that should be taken by the collectors before starting the carcass preparation: length of head+body+tail (A2), tail (C2), foot (D2), ear (F3), and the specimen's weight (Q17). Because these measurements are not always taken, this type of information is frequently wanting. I used these data as general indicators of size and dimorphism, but not in the geographical analysis. Their use can be problematical, since different collectors may use slightly different ways of measuring the animals.

PELAGE

A3 - limbs colour

B3 - tail colour

C3 - flanks colour

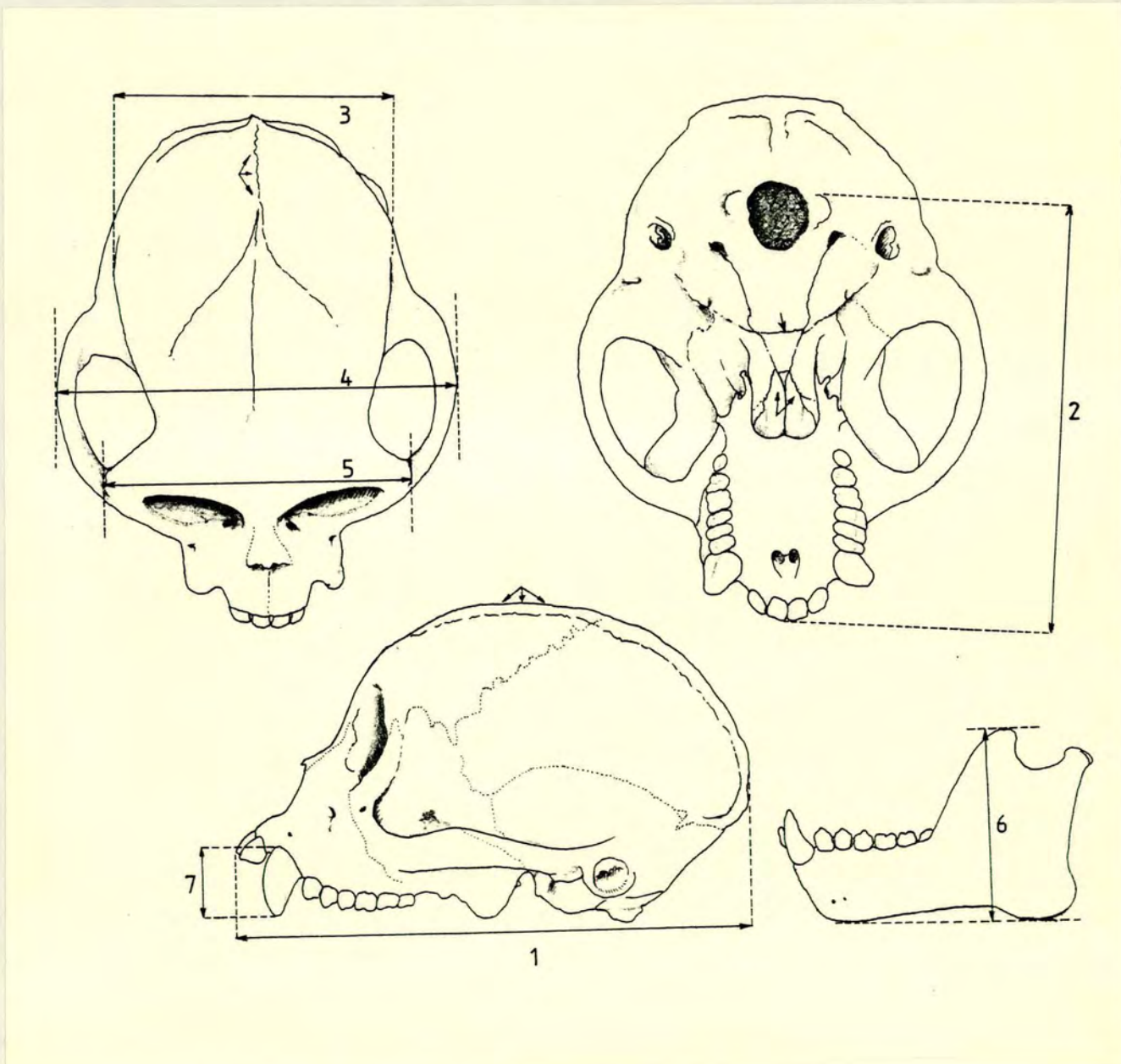
D3 - back colour

E3 - cap colour

F3 - cap shape

Pelage colour and cap shape have been used to separate Cebus forms by all taxonomists that have dealt with this group. The use

Fig.II.2 - Skull of C.apella showing the cranial characters considered in this study. Numbers 1 to 7 are various measurements (see text for details). The single arrow shows the spheno-occipital suture; the double arrow shows the vomer wings; the treble arrow shows the sagittal crest.



of pelage colour is not easy, however. It involves several difficulties which may affect the results. I will mention them briefly.

C.apella are brownish animals with darker limbs, tail and cap. Tail and limbs are generally of the same colour. The cap has often the same colour as the limbs and tail, but can be darker than them. The shade of the flanks and back varies considerably (more than the shade of the limbs, tail and cap); this variation can be used to distinguish animals from different regions. The differences in shade are not necessarily striking, and may be masked by individual variation. If it was possible to put side by side large samples from all regions, the subtlety of differences would not be a problem. This is not the case; the relevant material is scattered in a number of museums, and the various specimens have to be examined at different days and under different light conditions. Notes are then compared later on and subtle differences may not be detected. Also, the researcher's assessment of colours has to remain constant throughout data collection. This is probably true for categories like yellow and black, but may not be so for the various shades of brown. A standard colour code cannot be used because in these animals the general colour is not homogeneous, but given by the joint effect of hair banding and hairs of different colours being mixed in the coat.

The difficulties are not restricted to the researcher's own assessment of colours. Previous descriptions include terms like "clay-coloured", that do not necessarily mean the same for other researchers.

I tried to make my colour categories as distinct as possible.

I used six main categories: black, red, grey, brown, yellow and white. If the part under consideration did not fit into any of these, a modifier was introduced, e.g. reddish brown, brownish black, greyish brown. No doubt this system is subjective, but if gross differences exist between populations, the use of this system in a large sample should allow their detection.

Cap shape was initially classified as "divided into two high tufts", "divided into two low tufts", and "undivided". This method was soon discarded and substituted by a drawing of each cap in a frontal view. More detailed drawings were occasionally made, particularly of forms which seemed to be intermediate.

B. MAPPING OF THE LOCALITIES WHERE THE SPECIMENS WERE COLLECTED

The Cebus I examined were collected at 163 different localities. I made an attempt to determine their coordinates myself, and not to rely on the information provided by other researchers. In the cases where the coordinates had to be copied from the literature, the source of information is mentioned (see Appendix II.1).

The coordinates of most Brazilian localities could be found through the joint use of Vanzolini and Papavero (1968) and the 1:1,000,000 map of Brazil. Many of the collecting localities of the material housed at the Museu de Zoologia da Universidade de Sao Paulo could not be pinpointed without reference to Pinto (1945). Some localities were not easily located and odd sources of information had to be used. These included personal communications from collectors, expedition reports, old post code directories, old railway timetables, the U.S.A./C.I.A. localities index, and

P.Vanzolini's private localities file.

The precise location of collecting places is of obvious importance in the study of geographical differentiation. Therefore specimens with no precise origin had only limited value. Localities whose coordinates I was not completely sure of were discarded from the analysis. My sample includes mainly material collected in Brazil, other countries being poorly represented. Nevertheless, most of the geographical range of the "tufted" Cebus is covered in my sample; in terms of area of collection, it should encompass at least 13 of the 16 races accepted by Hill (1960).

C. DECISION AS TO WHETHER THERE IS ONLY ONE SPECIES INVOLVED

Hershkovitz (1949), Hill (1960) and Kellogg (according to Hill and Hershkovitz) treated all the tufted Cebus as a single species. Almost all other (earlier) taxonomists had treated the various forms as different species, some of which were implied to be sympatric (see for instance Vieira 1944).

The information available to Pusch (1941), Hershkovitz, Kellogg and Hill presumably allowed them to realize that the differences previously considered to be species-specific were either variations associated with age or with sex, or mere individual variation, and not a product of genetic isolation. These authors did not publish the details on which they based their conclusions, but if they had detected sympatry between the forms that they recognized, they would not have treated them as races. The absence of sympatry is not, however, a proof that the various forms are races. The acceptance of race status must be based on the existence of intergradation between the various forms. Hill, Hershkovitz and

Kellogg were probably able to define a morphological gradient between some (or all) forms, but this is not detailed in their published work. Hill (1960) mentions (p.438) the existence of hybrids between "most" races at the periphery of their ranges, but does not mention what they look like and which forms are in fact involved.

In my preliminary examination of the qualitative characters I detected morphological transition between several forms of the Atlantic forests. I suspected, although localities were too spaced for firm conclusions, that the same was happening in central Brazil and in the Amazon basin. Therefore I chose to analyse the information as if I was dealing with only one species. This is based on the assumption that the relatedness found in the forms of southeastern Brazil is similar to the relatedness among all the "tufted" forms. Another arrangement may be put forward as new information from critical areas becomes available.

D. POOLING OF THE INFORMATION YIELDED BY NEIGHBOURING LOCALITIES

Since the geographical analysis requires large samples, I tried to maximize the number of specimens to sample by pooling the information obtained at neighbouring localities. I only considered for pooling localities which were within a circle of 60 km diameter. If the localities considered for pooling were within a circle of 30 km diameter, and if between them there was no obvious geographical barrier like large rivers, the information collected at these localities was simply put together and treated as part of the same sample, the assumption being that the animals from these localities shared the same gene pool. The localities pooled in this way were:

AM2 and AM3; BA9 and BA10; ES4 and ES5; MA1, MA2 and MA3; MG11 and MG21; PA4 and PA25; PA8 and PA17; RJ1 and RJ2; SC1,SC2 and SC3; SP2,SP9 and SP14; SP12 and SP32; SP13 and SP18 (see full localities names in Appendix II.1).

If the localities under consideration for pooling were separated by more than 30 km, a one way analysis of variance (or a t-test when appropriate) was used to check whether the samples could be considered as part of the same population. This was done for each cranial character separately. The cases tested are listed in table II.1.

Other desirable poolings (e.g. MG2+MG7+MG10; SP24+SP29; SP20+SP5) could not be tested because the samples were too small to allow testing - these localities were therefore not pooled.

For brevity, I shall refer to only one of the pooled localities when mentioning the whole group (e.g. SC1 for SC1=2=3=4).

The sample size (circa 750 animals) may look large, but the species distribution is very wide, the sexes have to be treated independently and only adults can be used for morphometric characters analysis. Therefore, even after the pooling of information from neighbouring localities, only some of the samples were of acceptable size for quantitative analysis. I considered as acceptable a sample with at least four adult skulls of the same sex. Fig. II.3 shows the location of these "major" samples and indicates whether they are the product of pooling of information or not.

E. ANALYSIS OF THE VARIOUS CHARACTERS WITHIN THE MAJOR SAMPLES

Before comparing samples from different localities, it is

TABLE II.1
TESTS FOR LOCALITY POOLING

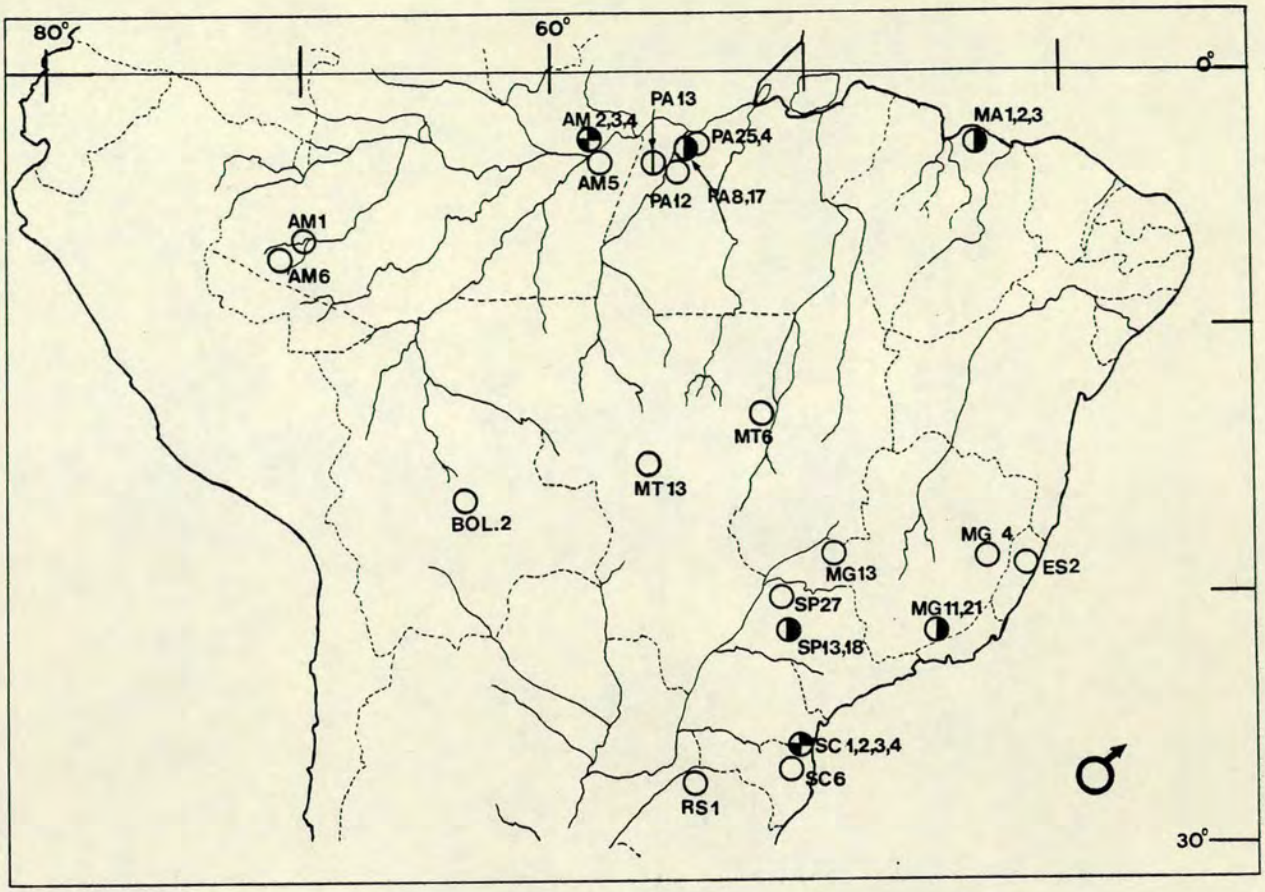
LOCALITIES UNDER TEST	SEX	IS THE POOLING ACCEPTABLE FOR ALL CHARACTERS? (ONEWAY ANOVA) p<0.01	p<0.05	DECISION
AM2&3 + AM4	Females	----Insufficient sample---		Localities
	Males	Yes	Yes	were pooled
SP6 + SP22	Females	Not for K1	Not for J1,K1	Localities
	Males	Yes	Not for G1	not pooled
MT9 + MT13	Females	Yes	Not for I1	Localities
	Males	Yes	Not for H1,H1,J1	not pooled
SC1&2&3 + SC4	Females	Yes	Not for H1	Localities
	Males	Yes	Yes	were pooled

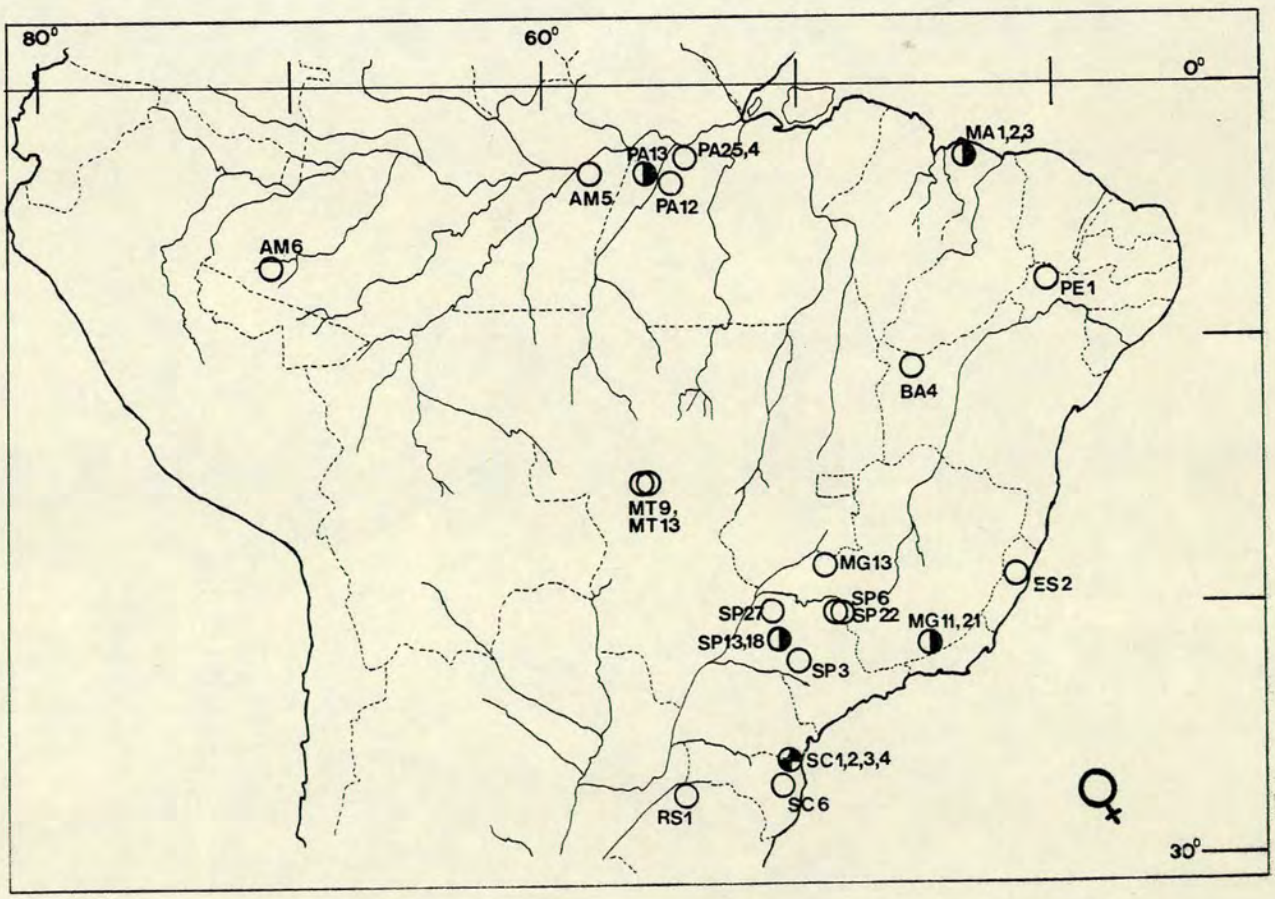
Fig.II.3 - Major samples for skull characters. See Appendix II.1 for the full names of localities.

○ = sample is a single locality

◑ = sample is a pool of localities, one or more of which would be a major sample on its own.

◓ = sample is a pool of localities, none of which would be a major sample on its own.


80°
60°
0°
AM 2,3,4
PA 13
PA25,4
AM5
PA12
PA8,17
MA1,2,3
AM1
AM6
MT6
MT 13
BOL.2
MG 4
ES2
MG13
SP27
MG11,21
SP13,18
SC 1,2,3,4
SC6
RS1
30°


80°
60°
0°
MA1,2,3
PA13
PA25,4
AM5
PA12
AM6
PE1
BA4
MT9,
MT13
MG13
ES2
SP6
SP27
SP22
MG11,21
SP13,18
SP3
SC1,2,3,4
SC6
RS1
30°

necessary to check within samples whether any character a. changes with age; b. is different in the two sexes; c. is correlated with other characters. If there are variations associated with age or with sex either the sample has to be sub-divided (so that geographical comparisons are only made among animals of the same category) or corrections have to be introduced to compensate for the differences. If the characters examined are strongly associated, they should be treated as a single character, and, if multivariate techniques are to be used, they should be restricted to those that are not affected by character correlation.

a. SEXUAL DIMORPHISM (tested on adult animals)

Although for all the morphometric characters (G1, H1, I1, J1, K1, L1, N1, A2, C2, D2) there is an overlap of male and female values, males are noticeably larger than females. For some morphometric characters (e.g. braincase width) the overlap is wide; for others male and female values are almost invariably very different (e.g. canine size). See Appendix II.3. In the majority of these characters the differences are not obvious, so a oneway analysis of variance (oneway ANOVA) was used to check whether the differences between male and female mean values were significant. A summary of the results for the morphometric characters is shown in Table II.2.

For the other characters, the results are:

A3 to E3 - pelage colour

I checked for sexual dimorphism in pelage colour in the 50 samples (50 localities) which included at least one (adult) skin of

TABLE II.2
SEXUAL DIMORPHISM IN THE MORPHOMETRIC CHARACTERS

CHARACTER	PERCENTAGE OF LOCALITIES WHERE THE CHARACTER IS SIGNIFICANTLY DIMORPHIC	NUMBER OF TESTED LOCALITIES
G1	100	15
H1	100	15
I1	33	15
J1	100	15
K1	100	15
L1	87	15
N1	100	15
A2	43	7
C2	14	7
D2	83	6

each sex. I was unable to detect very consistent differences between the sexes. In the smaller samples there seemed to be some dimorphism, but I assumed this to be reflecting insufficient sampling, since in the 13 larger samples the variation within sexes encompassed the differences observed between sexes. I may have therefore underestimated dimorphism in the areas represented by small samples.

The most consistent pelage colour dimorphism I detected was in the localities of southern Brazil. At PR3, PR5, PR6, PR7, RS1, SC1 to 4, SC6, SP27, SP13+18, SP1 and SP28, adult females (but not males) may have white hairs intermixed with the dark hairs of the anterior back and flanks. These hairs seem to be more commonly found in older females, although they are not exclusively or necessarily found in them. This character is present in all samples from RS, SC and PR and in some samples from SP, and nowhere else.

F3 - cap shape

In the same samples where pelage colour was examined I checked for sexual dimorphism in cap shape. Only adult animals were considered; juveniles and infants do not have this character fully developed (see next section). Individual variation was generally large and only in some samples was it possible to establish a 'representative' cap shape. The only consistent difference between sexes that I was able to detect again comes from localities in southern Brazil, where some females, but not males, have a more forward-pointing or sideways-pointing tuft than males (e.g. in SC1 to 3, RS1, SP36, SP33, SP26, SP12). This type of tuft is found only occasionally and it may be that its apparent restriction to females

was a product of the small sample sizes. This form of cap can be found rarely in other areas of C.apella distribution, produced by unusual whorls in the cap, but only in southern Brazil (and particularly in the samples from SC) does it seem to be very common.

In central Brazil and along the Amazon river (PA) females seem to be more prone to develop tufts than males do. Their tufts also seem to be longer than those of males. However, as my samples are widely separated, it is difficult to establish the exact geographical distribution of this character.

M1 - vomer pneumatization

Despite its large individual variation, mean vomer pneumatization was different in males and females. In 10 out of the 16 localities for which there were sufficiently large samples of both sexes, males develop (on average) more pneumatized vomers than females do. See Appendix II.4 for "measurements".

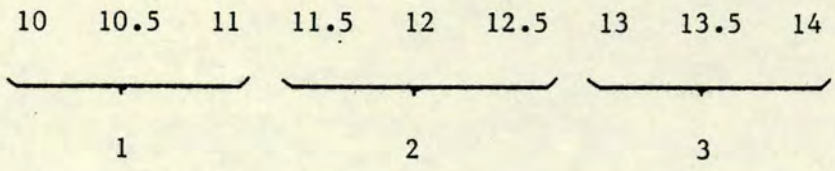
The real degree of dimorphism is not always the apparent one, because several characters are also dependent on age (even in adult life), and each sample included different numbers of males and females of various ages. However, all morphometric characters are significantly dimorphic in at least one of the tested localities (and half of them in all localities, as shown above). F3 and M1 (qualitative characters) also seemed to be slightly dimorphic. It is therefore convenient to treat the sexes separately during all geographic analysis. An exception can be made for pelage colour because this character does not seem to be strikingly dimorphic in any locality.

b. CHANGES WITH AGE

For each skull I noted the stage of tooth eruption or, in animals with complete permanent dentition, the wear of the first upper molars.

All the skulls available at the Museu de Zoologia U.S.P. (406 skulls: 82 of immature animals and 324 of adult animals) were used to build a "relative-age scale". This scale is a sequential arrangement of the various stages of tooth eruption and tooth wear (see Table II.3). This relative-age scale was then used to time morphological changes.

These changes may be of two kinds: changes associated with growth and changes during adult life. The variation due to growth is not considered in this study because I only used, for analysis, information from animals which had complete permanent dentition (age categories 10 onwards). At stage 10 Cebus are considered adults (e.g. by Napier 1976) and their growth should be over. However, I suspected, from the handling of the specimens, that variation in some characters (e.g. K1, L1) was linked to increasing age. To prove this it would be necessary to show that age-linked variations occur within localities. This was difficult to do because I established 9 age categories for adults and my largest sample from a single locality includes not more than 31 adults of each sex (all other samples are considerably smaller). To avoid this difficulty I grouped the nine adult age categories into sets containing 3 categories each, as shown below:



Even grouping the age categories into three sets, the information yielded by individual localities was not conclusive. Yet, as many samples seemed to consistently indicate some trends, it seemed reasonable to pool the information from all localities and test whether the apparent tendencies held for the species as a whole. The weakeness of this procedure is that different races may have different tendencies and the result derived from the pooled data may be affected by the differential representation of the various races. The results obtained with the pooled information are given in Table II.4.

Table II.4 indicates that considerable changes occur in Cebus apella anatomy even after the eruption of all permanent teeth, i.e., in a phase when growth is generally considered to be over. Several of the skull changes are similar in the two sexes. They involve the increase of J1,K1,L1,M1 and N1 mean values with increasing age (Fig. II.4). The increase in mean value seems to be followed by a reduction at old age in some cases. However, the sample size for old animals is quite small.

The vomer (in both sexes) also seems to undergo an increase in the mean inflation value. Della Serra (1950) had observed that vomer inflation increased as the animals matured, but he did not notice that the increase was maintained during mature life.

Some changes were restricted to males, e.g. the formation of a sagittal crest, and the increase in mean G1 and H1. As to the

TABLE II.3
AGE CATEGORIES FOR SKULLS OF CEBUS APELLA

The columns on the right associate the various categories with absolute time, based on information from (1) Kulhorn 1943,1953,1955 apud Hill 1960; (2) Napier and Napier 1967 apud Elias 1977; (3) Gilmore 1943; (4) Napier 1976. [mo = months]. Symbols: I-incisors; C-canines; P-premolars; M-molars (the same letters in lower case are used for milk dentition). Teeth are considered erupted when they are in occlusion. Specimens can be allocated to intermediate categories (e.g. 10.5).

CATEGORY	CHARACTERIZED BY	EXAMPLES	REAL AGE (1)	(2)	(3)	(4)
1	Any eruption stage of i,c,p up to stage iicp(p) / iicp(p)	SP 8959 SP 833 SP 3861	0 to 5 mo			INFANTS
2	m is emerging	SP 2382	6 to 7 mo		6 to 8 mo	
3	m are all erupted. M1 not yet emerging (no permanent teeth)	Olalla 951		6-8mo	from 6-8mo up to 14 - 18 mo	
3 to 4	M1 emerging OR M1 already erupted but with milk incisors	SP 1178 SP 8493 SP 868				
4	M1 all erupted, and i being substituted by I	SP 8905 SP 2859B				JUVENILES
5	All I erupted but M2 not yet emerging	SP 2218				
6	M2 emerging	SP 294				
7	M2 all erupted; M3 not yet emerging ; p not yet being substituted by P	SP 3860				
7 to 8	M2 all erupted; p are being substituted by P (in the females this is accompanied	SP 8450 SP 434 SP 2493 SP 10538			up to 36-40 months	

	by C eruption); M3 starts development	SP 10327 SP 11171	
8	P1,P2,P3 erupted; c are being substituted by C, or C are finishing eruption; at the same time M3 is emerging (in females the C may be totally erupted before M3 emerges.	SP 2715 SP 5130 SP 5918 SP 10500 MN 23519	
9	At least one M3 erupted. Sequence 8 to 9 is slightly artificial since an animal may reach 9 without going through 8 (e.g. SP 1823)	SP 8920 SP 10497 SP 10534	up to 42 months
10	Complete permanent dentition. M1 have nitid pointed cusps.In males C may not be fully erupted.	SP 7133	36 to 40 months
11	Dentition as in 10,but M1 cusps are polished, not as sharp as 10.	SP 5192	up to 8/10 years
12	Dentition as in 10,but wear produces pit(s) on M1 cusp(s) tip(s) (usually on the lingual side)	SP 6324	ADULTS
13	Dentition as in 10,but wear creates depressions on M1 cusp(s) tip(s) (usually on the lingual side)	SP 10540	
14	Dentition as in 10,but M1 are almost completely worn (flat surface)	SP 2386	up to ?20 years

TABLE II.4

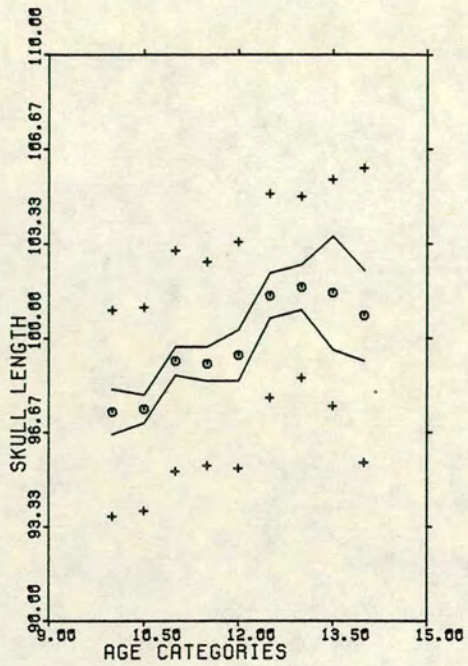
	DO CHANGES OCCUR BEFORE ADULTHOOD? (age categ. up to 10)	DURING ADULT LIFE? (age categories from 10 to 14) MALES	FEMALES
E1	NO, always absent.	YES, develops in most males. By age categ. 12, 80% of males have a sagittal crest	NO, almost always absent; only two cases of slightly crested females in 155 examined skulls
G1	YES, growth.	YES, significant differences among age categories.	NO significant differences among age categories.
H1	YES, growth.	YES, significant differences among age categories.	NO significant differences among age categories if categ.10 through 14 are tested, but YES if these categories are grouped into 3 sets.
I1	YES, growth.	NO significant difference among age categories.	NO significant difference among age categories.
J1	YES, growth.	YES, significant differences among age categories.	YES, significant differences among age categories.
K1	YES, growth.	YES, significant differences among age categories.	YES, significant differences among age categories.
L1	YES, growth.	YES, significant differences among age categories.	YES, significant differences among age categories.
M1	YES, growth and change in mean pneumatization.	YES, change in mean pneumatization.	YES, change in mean pneumatization.
N1	YES, eruption and substitution of teeth.	YES, significant differences among age categories.	YES, significant differences among age categories.
O1	NO, remains open.	YES, closes between	YES, closes

		age categ.9 and 13. At categ.13, 75% of animals have closed sutures.	between age categ. 9 and 12. At categ. 11, 75% of animals closed sutures.
A2> C2> D2>	YES, growth	NOT TESTED	NOT TESTED
A3> B3> C3> D3> E3>	NO consistent changes observed.	NO consistent changes observed.	White hairs may develop on the flanks of old females; only in some localities.
F3	YES, changes in shape.	YES, changes in shape and in hair length.	YES, changes in shape and in hair length.

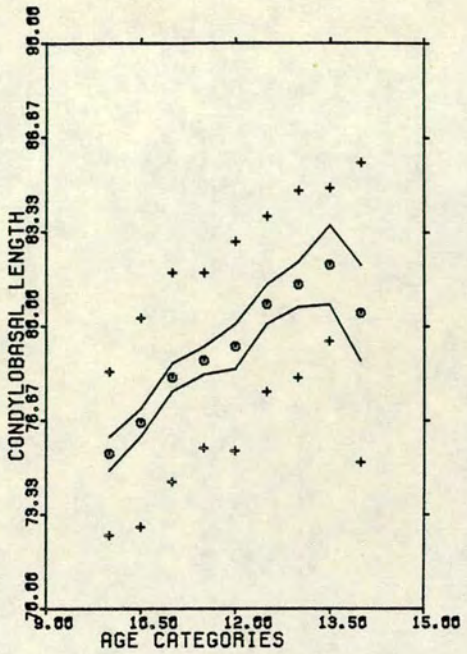
The significance of differences among the means at various ages was tested only for adults (second and third columns) using the LSD procedure of S.P.S.S. ONEWAY subprogram at p=0.05 (Nie et al. 1975). No tests were performed for juveniles. Tests were performed twice: 1. the means of the 3 sets of ages were compared; 2. the means of each age category were compared. Results were generally the same, and the one exception (H1-females) is mentioned in the table.

Fig.II.4 (A to L) - Graphs showing character mean in each (adult) age category. Only the characters which change significantly with age are shown. In all graphs except those of M1 (which includes only means), two confidence limits are indicated:

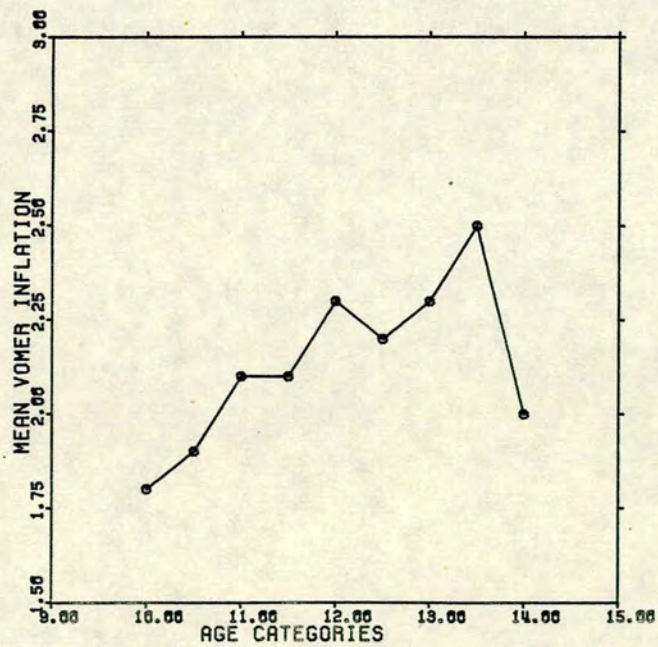
- mean plus and minus the standard deviation (crosses)
- mean plus and minus the mean uncertainty (lines). The mean uncertainty is the mean divided by the square root of n.



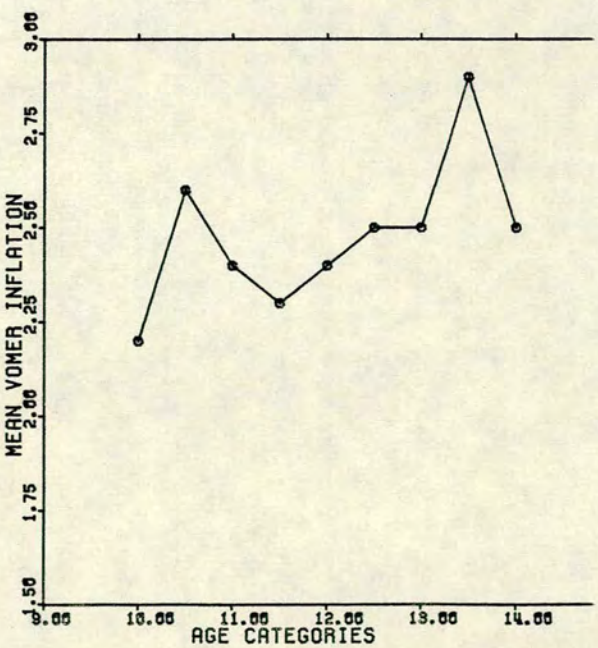
A. MALES - G1



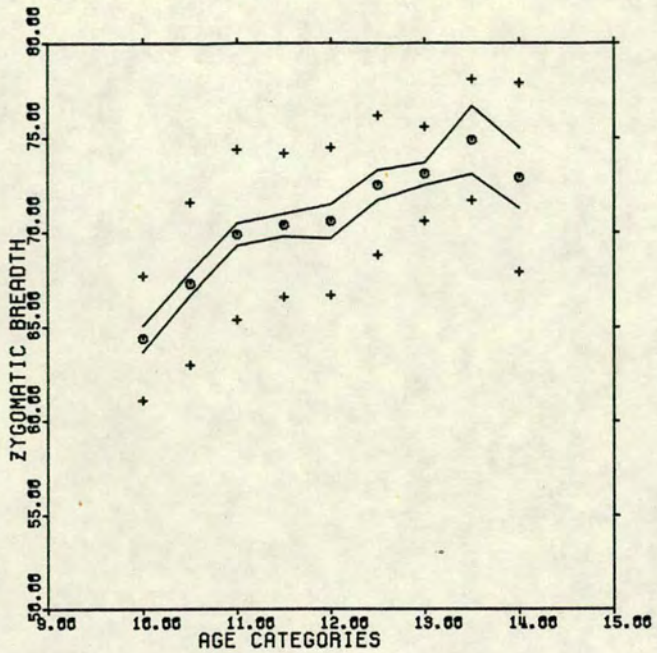
B. MALES - H1



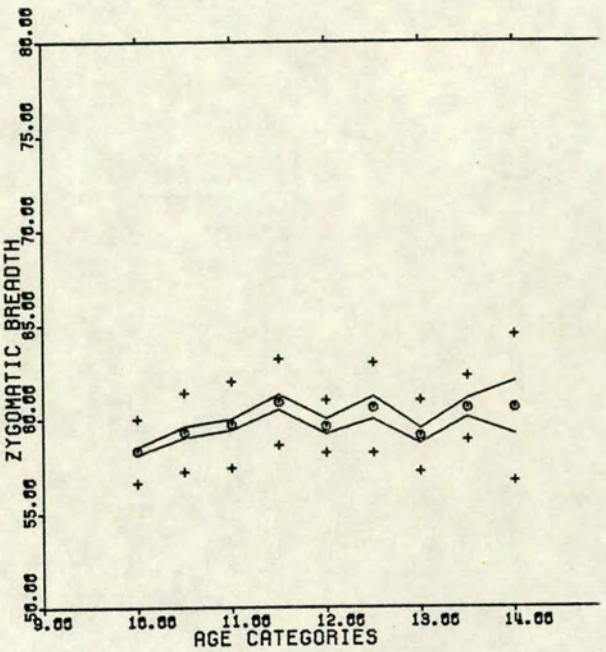
C. FEMALES - M1



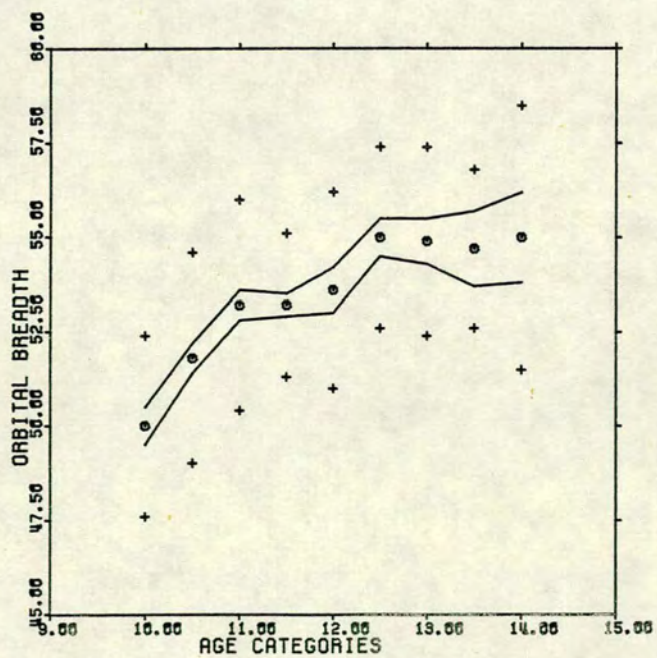
D. MALES - M1



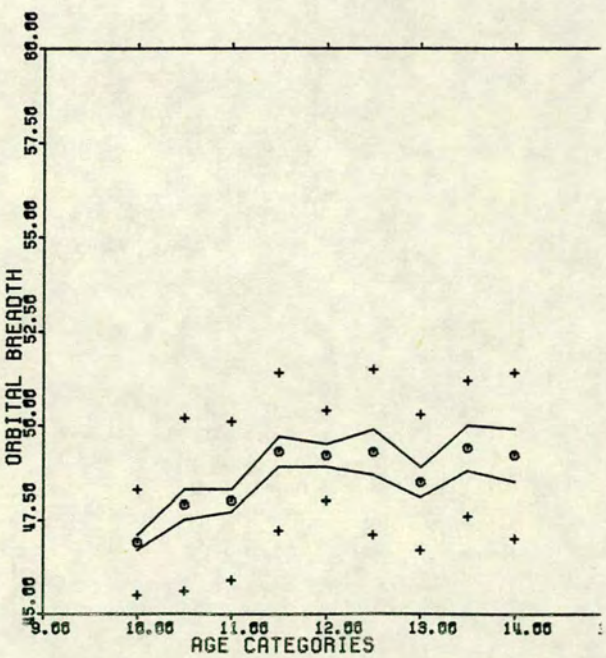
E. MALES - J1



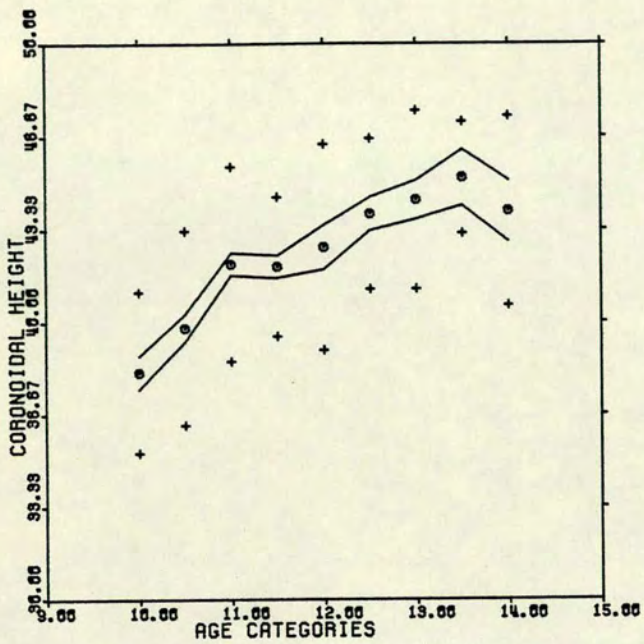
F. FEMALES - J1



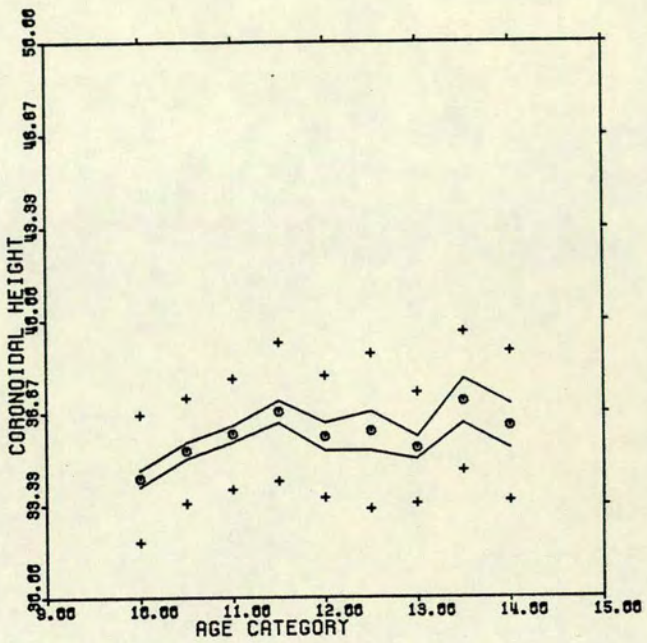
G. MALES - K1



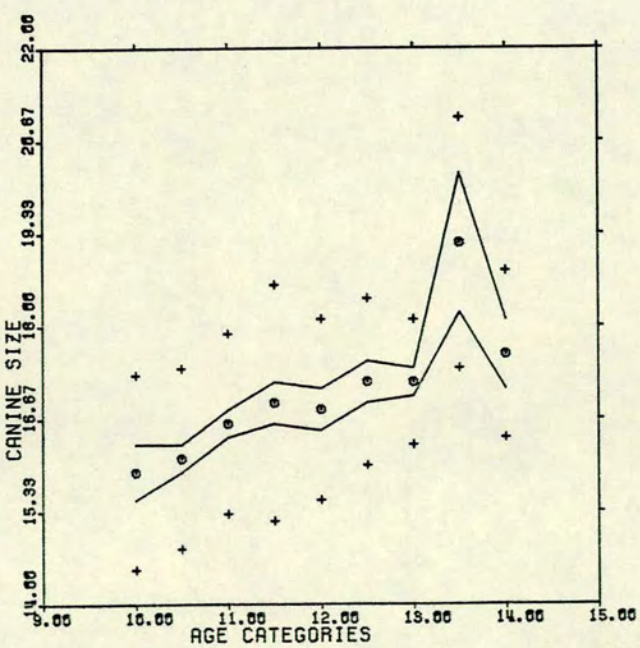
H. FEMALES - K1



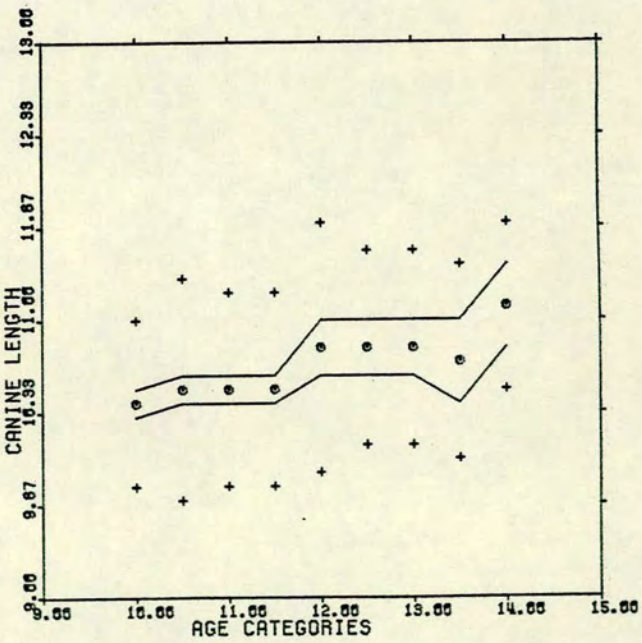
I. MALES - L1



J. FEMALES - L1



K. MALES - N1



L. FEMALES - N1

pelage, cap shape changes and tufts of longer hairs may develop during the same ('adult') period (Fig.II.5).

It cannot be proved that each sample is following the trend shown above. However, it is possible to check whether the result given by the pooled information is not artificial by dividing the total sample into two blocks and examining whether the trends still hold in the blocks. I divided my sample into "Amazonian"(AM) and "Atlantic"(AT) blocks. According to previous taxonomic work, each block should include more than one race, therefore the blocks should be reflecting the tendencies of more than one form. The results of this check are shown in Table II.5, which indicates that both blocks are quite consistent in showing age-linked changes in skull measurements. Although it also suggests that Atlantic and Amazonian females may differ in the changes of Hl, this does not alter the general picture.

The two blocks are also consistent in showing other age-linked changes which are not included in the table: F3,El. For the vomer inflation, however, the division of the sample into two blocks resulted in the loss of the pattern revealed by the pooled data; the separate blocks failed to show progressive increases in mean vomer inflation. Either there is much individual variation (and a very large sample would be required to reveal a trend), or the pattern shown by the pooled information is indeed artificial. I believe that in some races there is in fact an increase in vomer pneumatization; in others it is either non-existent or less pronounced. This will only be demonstrated with larger samples.

A comment should be made on the nature of these changes.

F3 - It is difficult to be sure of the functional aspects of the

Fig.II.5 - Cap shapes at different ages. Top row is based on sample SP-27 (Fernandópolis), and bottom row is based on sample ES-2 (Linhares). Specimens were selected to illustrate what seems to be the general trend, but there is more variation than is pictured. Age categories are indicated for each specimen. The sex is indicated when known.

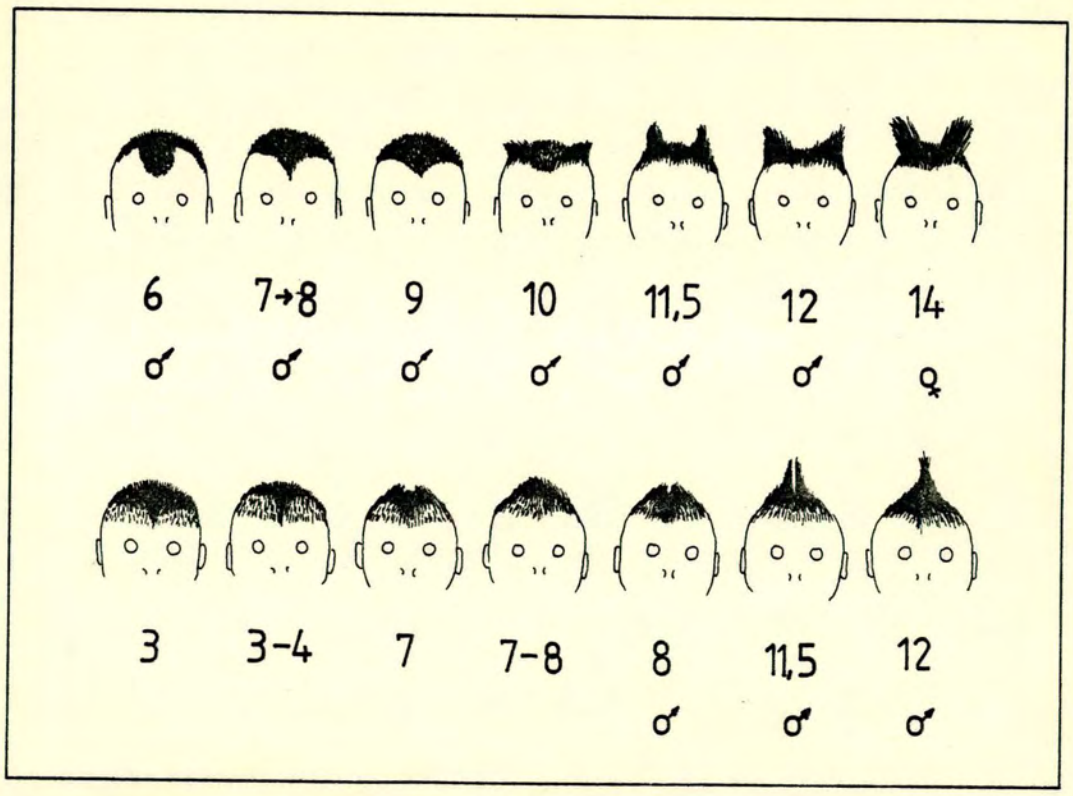


TABLE II.5

ARE THERE SIGNIFICANT DIFFERENCES BETWEEN MEAN VALUES AT DIFFERENT (ADULT) AGES?							
	MALES				FEMALES		
	AM (n=96)	AT (n=67)	AM+AT (n=163)		AM (n=71)	AT (n=98)	AM+AT (n=169)
G1	Yes	Yes	Yes	G1	NS	NS	NS
H1	Yes	Yes	Yes	H1	NS	Yes	Yes
I1	NS	NS	NS	I1	NS	NS	NS
J1	Yes	Yes	Yes	J1	Yes	Yes	Yes
K1	Yes	Yes	Yes	K1	Yes	Yes	Yes
L1	Yes	Yes	Yes	L1	Yes	Yes	Yes
N1	Yes	Yes	Yes	N1	Yes	Yes	Yes

(age-categories 10 to 14 re-grouped to form 3 sets instead of 9, as explained in the text. Test: L.S.D. procedure in SPSS ONEWAY subprogram, $p<0.05$) AM='Amazonian' group. AT='Atlantic'group.

development of hair tufts. Maybe the various cap shapes have social importance, allowing immediate distinction of the various age classes. Age-linked changes in the cap are not exclusive to this species. Similar trends have been described for at least 3 of the 4 accepted species of Cebus (Izawa 1980 for C.apella, Oppenheimer 1969A for C.capucinus, Robinson 1981 for C.nigrivittatus).

M1 - No easy explanation can be given for the increasing inflation of the vomer wings. Hershkovitz (1977, p.147) suggested that paranasal pneumatization is a way of enlarging bone surface area without increasing weight or losing strength, and that this surface increase might allow for more muscle attachment or for a better accommodation of organs in a skull with allometric changes.

N1 - The increase of canine size with age is surprising since teeth are subject to extensive wear and one would expect a reverse trend to occur. The observed pattern can be explained either by canine continuous growth or by the retraction of the alveolar edges. I made no detailed observations on the alveoli, so I can not check whether the observed trend is due to alveolar retraction; continuous growth of the canine is not unlikely, however. Nellis et al. (1978) showed that this happens in coyotes. Not having measured teeth with missing tips I may have eliminated the masking effect of wear.

E1, J1, K1, L1 - These characters (sagittal crest, zygomatic breadth, orbital breadth and coronoidal height) also show age-linked increases. All these changes could be forced by an enlargement of the jaw adductor muscles (temporalis, masseter, zygomatico mandibularis). Sagittal crests provide more area for insertion of the temporal muscle when the braincase is not sufficiently large (Romer & Parsons 1977, p.230). The development of the zygomatico

mandibularis produces an outbowing of the zygomatic arch (Hill 1960, p.25). Increases in the masseter muscle require more insertion area in the jaw and a wider zygomatic gap. Skull changes associated with the masticatory system have been observed in several primate species (Oyen and Enlow 1981). These authors showed that in several primate species the browridge and the nuchal region may undergo concomitant histological alteration which these authors attributed to 'growth related' changes in the masticatory system. They explained the changes in terms of growth because they did not investigate differences within the adult class - it was assumed that changes did not occur after maturation. What would cause the mastication muscles to enlarge in adults is not clear. Most of these changes are not restricted to the larger males, so they do not seem to be due sexual selection. They may be associated with an increase of weight throughout adult life (there is some evidence for this - weights of adult Cebus from southeastern Brazil seem to be constantly rising with age - information from the labels attached to specimens collected by the Yellow Fever Research Service around 1949).

Although the enlargement of masticatory muscles does not seem to be a product of sexual selection, the increase in G1, only detected in males, may be. Also, if the larger size of males is a product of sexual selection, the appearance of a sagittal crest may be an indirect product of it, since it may be due to allometric increase of muscle volume between males and females.

Whatever the cause of these changes, what is relevant for this work is that they are a source of non-geographical variation which calls for correction before comparisons are made between samples

from different localities.

This correction was done through the standardization of all adult measures to age category 12. To do this I used a computer program borrowed from M. Assumpção. The program was originally developed to solve a geophysical problem which has parallels with the one presented here. It basically determines, for each character, the curve that best describes its age changes, and then, given a value of any age, searches for the curve value corresponding to age category 12. A full description of the program would be tedious and superfluous, but a brief explanation of the various steps is given below:

I. an "initial curve" is determined where each age corresponds to a mean calculated with all available measurements for that age (i.e. data from various localities are put together). An iterative process follows (steps II to IV).

II. each sub set of data (a sub set consisting of all animals from one locality) is fitted to the "initial curve". This compensates for differences in general size between animals of different localities in the following way: if the animals from one sub set are on average different from the "initial" mean (e.g. if they are, on average, 5% larger than the "initial" mean) this amount is deducted from each value of the sub set.

III. after all sub sets have been fitted as described in II, new means are calculated for each age, and a "new curve" is thus established.

IV. steps II and III are repeated n times (n=4 in this study). At each time revised values are used for each sub-set (derived from the previous cycle). After these iterations a "final curve", which

should approach the best possible curve for the species, is obtained.

V. each individual (raw) value is then extrapolated to age 12 using the "final curve".

VI. all extrapolated values from one locality are then considered together and a standardized mean value for that character in that locality is thus obtained. The same is done for each of the remaining localities.

The means thus obtained, and their corresponding standard deviations, are now ready to be used in the geographic analysis.

A last comment should be made about this correction. Because both the "AM" and "AT" blocks of data are consistent in showing character changes with age, I assumed that the same trend was true in every locality. Although this is reasonable, given the nature of the changes, I provide no proof that this is the case. It may be that in some areas the animals do not change with age, or that they do it with different intensities. In these cases, if they exist, the correction I introduced would be distorting the real measures to an unknown extent.

c. CORRELATION BETWEEN CHARACTERS

Thorpe (1976, p.452) recommends that ontogenetic changes should be compensated before one checks for association between pairs of characters within the samples. This was done by the standardization of all measurements to age category 12. I then calculated the correlations between all variables within the major samples. This step is necessary because characters which are strongly correlated in all samples should be treated as a single

character. Also, if the correlation between two given characters is not present in all samples, the geographical pattern of correlations may give an insight on the separation of races.

I only looked for correlations between skull measurements; body measurements are not reliable for geographical analysis because of the differences in the collectors' measuring procedures. All other characters were either purely qualitative or semi-qualitative.

I decided to use a minimum of $r=0.8$ with $p<0.05$ as indicative of a "strong" correlation.

There were no pairs of characters strongly correlated in all tested localities. The proportion of localities in which a pair of characters was correlated varied from 0% to 35% in females and from 0% to 52% in males (see table II.6).

I checked whether the correlations followed geographical patterns, but was unable to detect any. The frequency of significant correlations between characters did not seem to be affected by sample sizes, since samples with as little as 5 individuals showed as many or more significant correlations than samples with 30 individuals. Yet, the pairs are not correlated at random: although all pairs were much more frequently correlated in males than in females, the characters more frequently correlated were the same in males and in females. The Spearman rank correlation coefficient between the values of corresponding cells in the male and in the female matrices is 0.71 ($p<0.001$). This indicates that there are real trends of character association, similar in males and females. Why the correlations are consistently more frequent in males is difficult to explain.

Since there seems to be a pattern of character association, it

TABLE II.6

Correlation between characters within samples ("intralocality correlations"). Each cell shows the percentage of localities in which the pair of characters was correlated with $r>0.8$ and $p<0.05$. All the major samples were tested, but as in some localities there was no information about a particular variable (e.g. all animals in the sample had broken teeth), the total number of localities tested varied from cell to cell. For males the number of tested localities varied from 19 to 21. For females the number of localities was 20 for all cells.

MALES

	G1	H1	I1	J1	K1	L1	N1	CHARACTER AVERAGE
G1	---	52.4	19.0	28.6	15.0	9.5	10.5	22.5
H1		---	9.5	38.1	25.0	23.8	15.8	27.4
I1			---	9.5	5.0	9.5	0.0	8.8
J1				---	35.0	38.1	21.0	28.4
K1					---	19.0	21.0	20.0
L1						---	10.5	18.4
N1							---	13.1

Average of all cells.....19.8

FEMALES

	G1	H1	I1	J1	K1	L1	N1	CHARACTER AVERAGE
G1	---	35.0	5.0	5.0	10.0	0.0	5.0	10.0
H1		---	10.0	15.0	15.0	5.0	5.0	14.2
I1			---	0.0	5.0	0.0	0.0	3.3
J1				---	20.0	15.0	0.0	9.2
K1					---	10.0	15.0	12.5
L1						---	5.0	5.8
N1							---	5.0

Average of all cells.....8.6

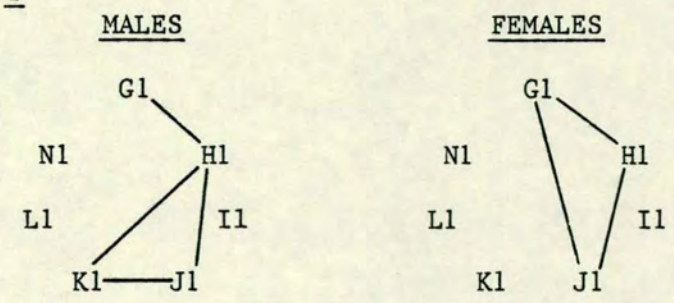
is now necessary to determine how strong should the association be for the characters to be considered redundant. At this point researchers are generally forced to make an arbitrary decision (as did Vanzolini and Williams 1970, Cerqueira Silva 1980). I followed Thorpe's suggestion (1976, p.418-419) that the characters to be discarded from analysis should be the ones correlated both "intra-locality" and "inter-locality". A summary of the "intra-locality" correlations is given in Table II.6. The "inter-locality" correlations can be calculated in one of two ways:

1. using mean character values (as many means as there are major samples). In this case each point on the graph corresponds to a locality's average. This method has the disadvantage that it gives equal importance to samples of different sizes.

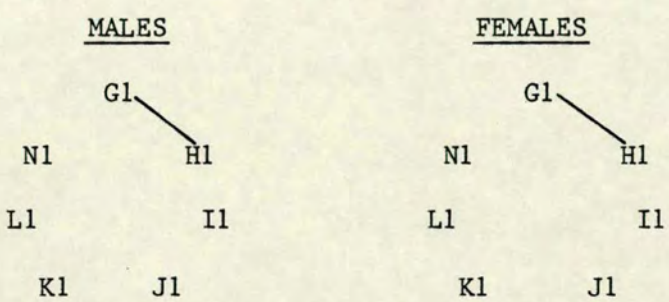
2. using individual measurements - in this case each point on the graph corresponds to one animal. This method has the disadvantage that a very large sample from one single locality will affect the final result more than with method 1.

The results of these two methods are shown below. Lines unite the characters which are correlated with $r>0.8$ and $p<0.05$.

METHOD 1 -



METHOD 2 -



The difference between the results of the two methods is not as strong as it appears. If we add, to the results of Method 2, lines uniting characters correlated with $r>0.7$, the pattern matches that of Method 1.

For the "intra-locality" correlation (Table II.6) it is necessary to choose what is a significant number of instances in which a pair of characters is correlated. To use the same minimum for males and females did not seem convenient, for, although both sexes seem to be showing the same pattern of character association, the pattern is more easily detected in males. I therefore decided to select, in each matrix, those values which seemed particularly above the matrix average. With this method the problem of imposing the same absolute minimum for males and females is avoided, and only the characters that are particularly strongly correlated are selected. In a study where all morphometric characters are skull

measurements, one should expect that striking changes in one character should, at least to some extent, affect the others. In this sense, all or almost all the characters are associated, but it is unlikely that all are redundant. By selecting the values which are well above the matrix average, we select the characters which are more likely to be redundant. The decision about what is "well above" is rather subjective. By inspecting the matrices (Table II.6) I decided that only the pair G1-H1 had a particularly strong association. Both in males and females these characters are associated 2.5 times more frequently than the average association between all characters. As these two characters are also strongly correlated between localities, one of them can be considered redundant. To represent the pair I chose G1 because, on average, it correlates less with the remaining characters.

F. ANALYSIS OF THE CHARACTERS BETWEEN LOCALITIES

The comparison between samples aims at defining groups of localities where the animals share a number of characters not found elsewhere, or where the animals are on average more similar among themselves than they are to animals from other areas. A higher similarity supposedly reflects a closer relatedness. To investigate such similarity, qualitative characters had to be treated differently from quantitative ones. Each character provided its own pattern of "related localities", which were then superimposed and interpreted. To facilitate reading, only a brief description of the methods will be given here, and details of the methods will be presented together with the results, each character considered separately.

- Quantitative characters

The morphometric characters were all skull measurements (G1,H1,K1,L1,N1). H1 was discarded during univariate analysis because of its correlation with G1. Corrections for age had already been introduced for the characters which required them. Sexes were treated separately. Data were then treated in two ways:

-- each character considered individually (univariate analysis)

-- characters considered together (multivariate analysis)

- Qualitative characters

For each locality I described each character, including an indication of how variable it was. A shortened version of these descriptions is given (only for samples with at least 4 specimens) in Appendix II.5. The information for each locality was written on a map, close to the corresponding locality, and I then looked for morphological aspects which neighbouring localities might share. These maps (containing indications of the variation in each locality) will not be presented here, but only the patterns that I was able to discern in them.

Colour of limbs will not be mentioned in the results because, besides not being variable enough across regions, it seemed to be redundant with the character cap colour.

Cap shape could only be studied in adult animals; this was not the case for pelage colour, since this character does not seem to change strikingly with age.

- Semi qualitative characters: vomer pneumatization, and sagittal

crest height

Only adult skulls were used.

The mean vomer pneumatization in each major locality was indicated on a map, (males and females analysed separately)

Any notes I had on sagittal crest height were transfered to a map, near the corresponding locality.

Patterns were then sought in each map.

RESULTS

Appendix II.4 summarizes the quantitative data in the major localities.

Appendix II.5 summarizes the qualitative data for samples with at least four skins (4 adult skins for cap shape).

A large part of the results are contained in Figures II.7 to II.26. The results will be considered first in isolation (each character separately) and then I will consider the pattern indicated by all characters together.

Quantitative characters (considered individually)

After checking that there were significant differences among the character means of the various localities (one-way analysis of variance), a multiple comparison test was performed for each character. I used the Student- Newmann-Keuls (S.N.K.) test (available as part of the S.P.S.S. subprogram ONEWAY) (Nie et al. 1975) to obtain the sets of means which are not significantly different. The same test was chosen by Sokal and Rinkel (1963) in their study of aphid geographical variation.

The localities which correspond to the lowest, highest and intermediate sets of means were then indicated on maps (Figs. II.7 to II.12). This was done by shading the areas around the localities according to the group they belonged to. The criterion for defining the lowest, highest and intermediate groups was copied from Sokal and Rinkel (1963). The relevant cases are pictured in Fig. II.6.

I avoided drawing isophenes on the basis of the S.N.K. sets (as Sokal and Rinkel (1963) did) because I felt that extrapolation

Fig.II.6 - Schematic diagrams showing the shading conventions used to present the results of the S.N.K. tests. A to F represent means of increasing values. Three groups of means (low, high and intermediate) are recognized. The lines to the left of each block unite the means which are not significantly different.
The third block shows a case in which two adjacent subsets are separated by a gap (so that all members of one subset are significantly different from all members of the next one. In cases like this a thick, dark line was used to encircle the localities of the isolated group.
These conventions were used in Figs II.7 to II.12

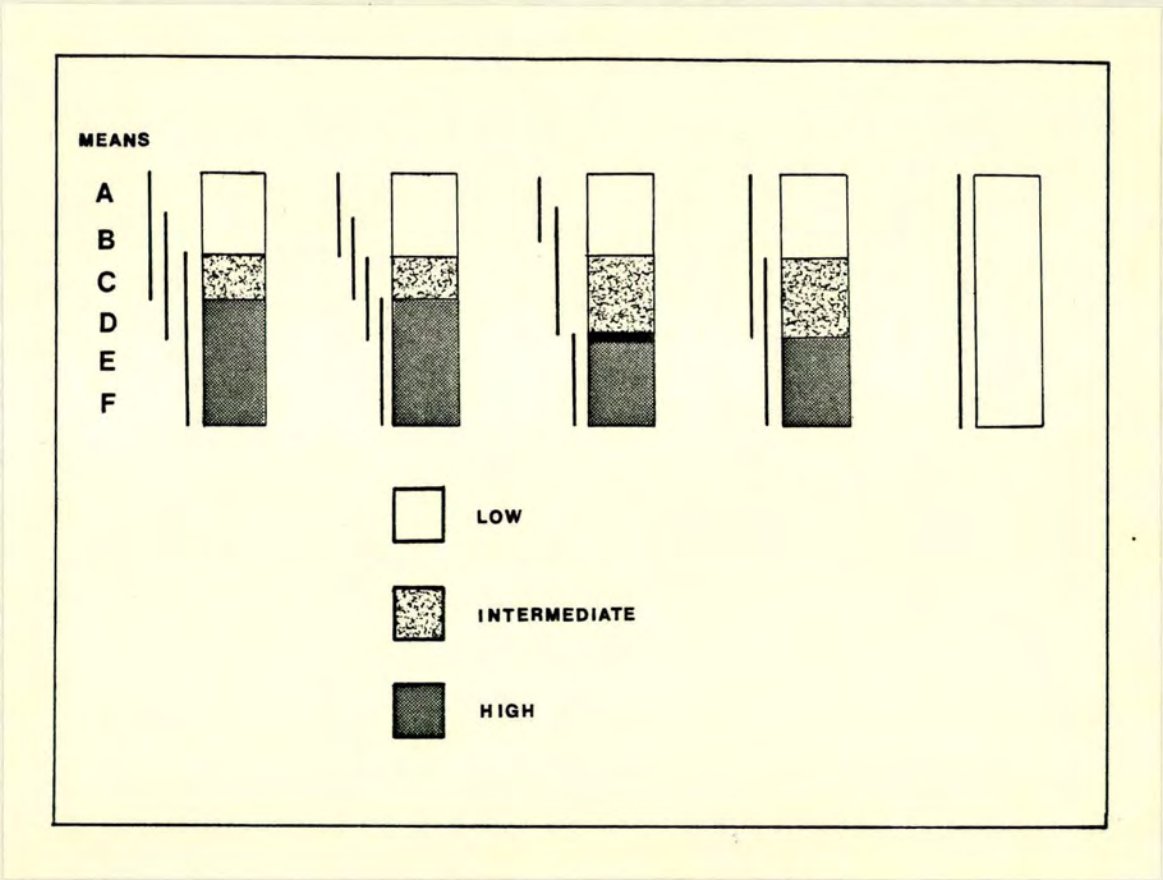
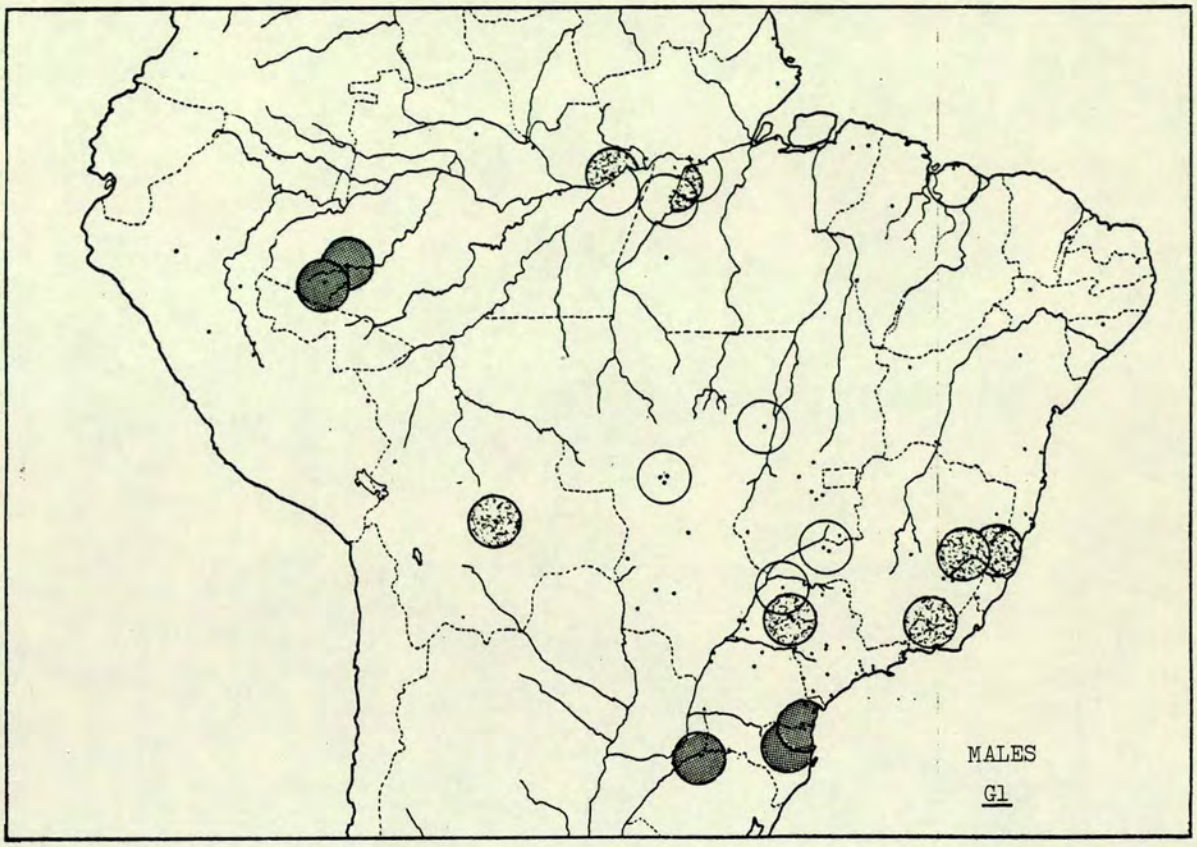


Fig. II.7 - Geographical variation of character G1 (skull length)

Shading code as in Fig.II.6. Localities as in Fig.II.3. The means in each locality, and the subset they belong to are:

MALES			FEMALES		
LOCAL.	MEAN	SUBSETS	LOCAL.	MEAN	SUBSETS
MT6	95.0		MT9	86.4	
SP27	96.8		PA13	87.5	
PA25	97.8		MA1	88.1	
MA1	97.9		PE1	89.2	
PA12	97.9		MG13	89.3	
PA13	98.0		PA4	89.8	
MT13	98.5		BA4	90.2	
MG13	98.6		AM5	90.4	
AM5	98.6		SP22	91.1	
SP13	99.0		PA12	91.5	
MG4	99.3		MT13	91.5	
AM2	99.3		SP3	92.0	
ES2	99.5		SP27	92.1	
PA8	99.9		MG11	92.2	
MG11	100.4		RS1	92.9	
BOL-2	101.8		SP6	93.0	
AM6	102.0		SP13	94.3	
RS1	103.7		ES2	94.4	
SP22	103.9		SC6	94.6	
SC1	104.0		SC1	96.8	
AM1	104.6		AM6	97.4	
SC6	105.0				


MALES
G1

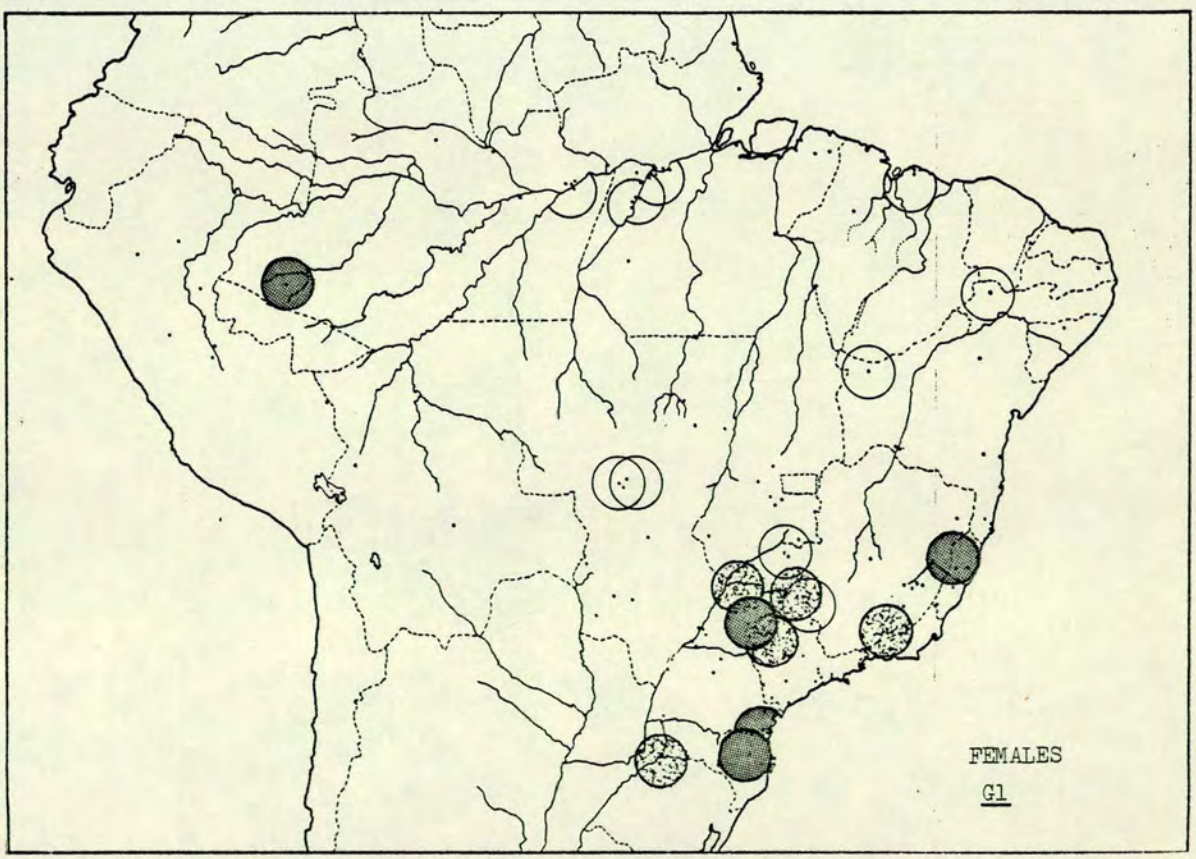
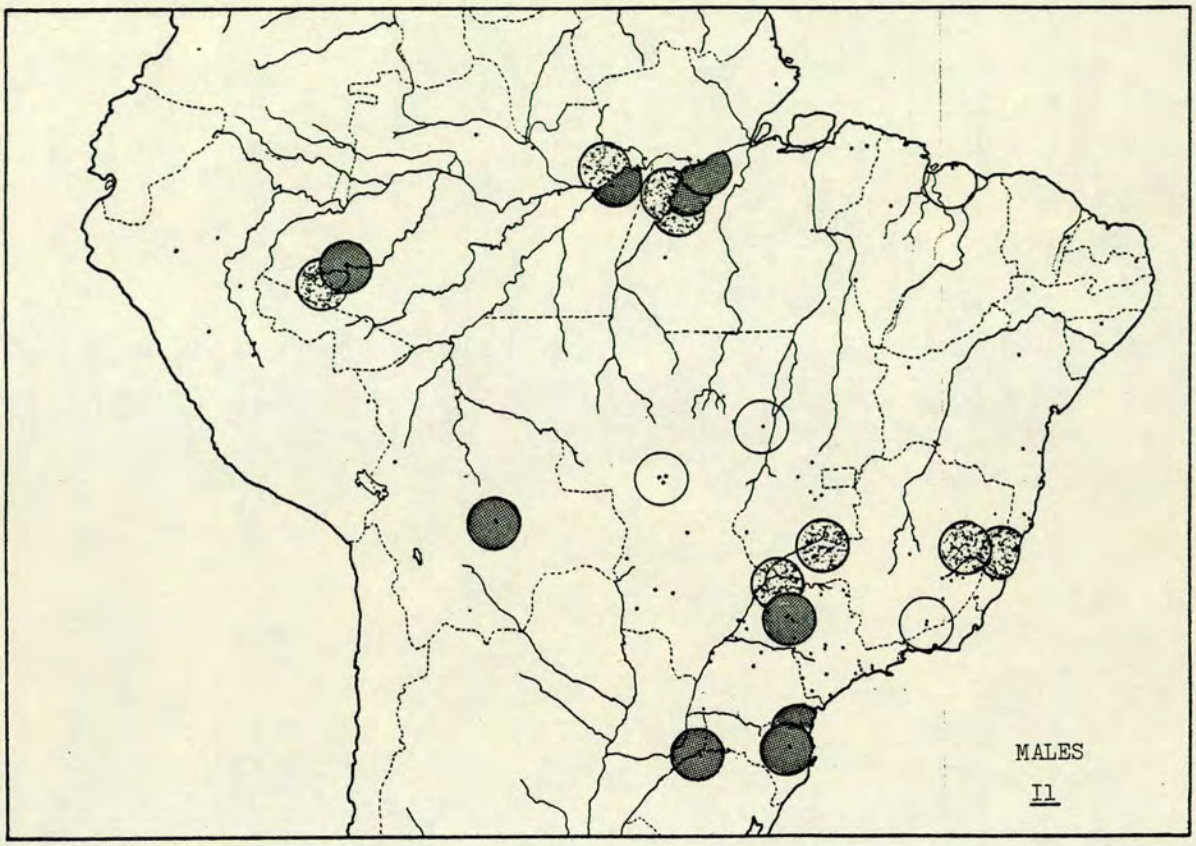

FEMALES
G1

Fig.II.8 - Geographical variation of character I1 (skull breadth)

Shading code as in Fig.II.6. Localities as in Fig.II.3. The means in each locality and the subsets they belong to are:

MALES			FEMALES		
LOCAL.	MEAN	SUBSETS	LOCAL.	MEAN	SUBSETS
MT6	48.3		MT9	47.6	
MG11	50.0		MG11	48.1	
MA1	50.7		PE1	48.7	
MT13	51.6		PA13	49.2	
ES2	51.6		ES2	49.8	
MG4	51.6		MT13	50.0	
AM2	51.8		MA1	50.2	
SP27	51.8		SP22	50.2	
MG13	51.8		MG13	50.4	
PA13	51.9		AM5	50.4	
AM6	52.0		BA4	50.5	
PA12	52.0		PA4	50.7	
SP22	52.1		RS1	50.8	
PA4	52.1		PA12	50.9	
AM5	52.4		SP13	51.1	
SP13	52.8		SP27	51.2	
RS1	52.9		SP3	51.4	
BOL-2	53.0		SC6	51.6	
SC1	53.1		AM6	51.7	
PA8	53.2		SC1	52.1	
SC6	54.5		SP6	52.2	
AM1	54.6				


MALES
I1

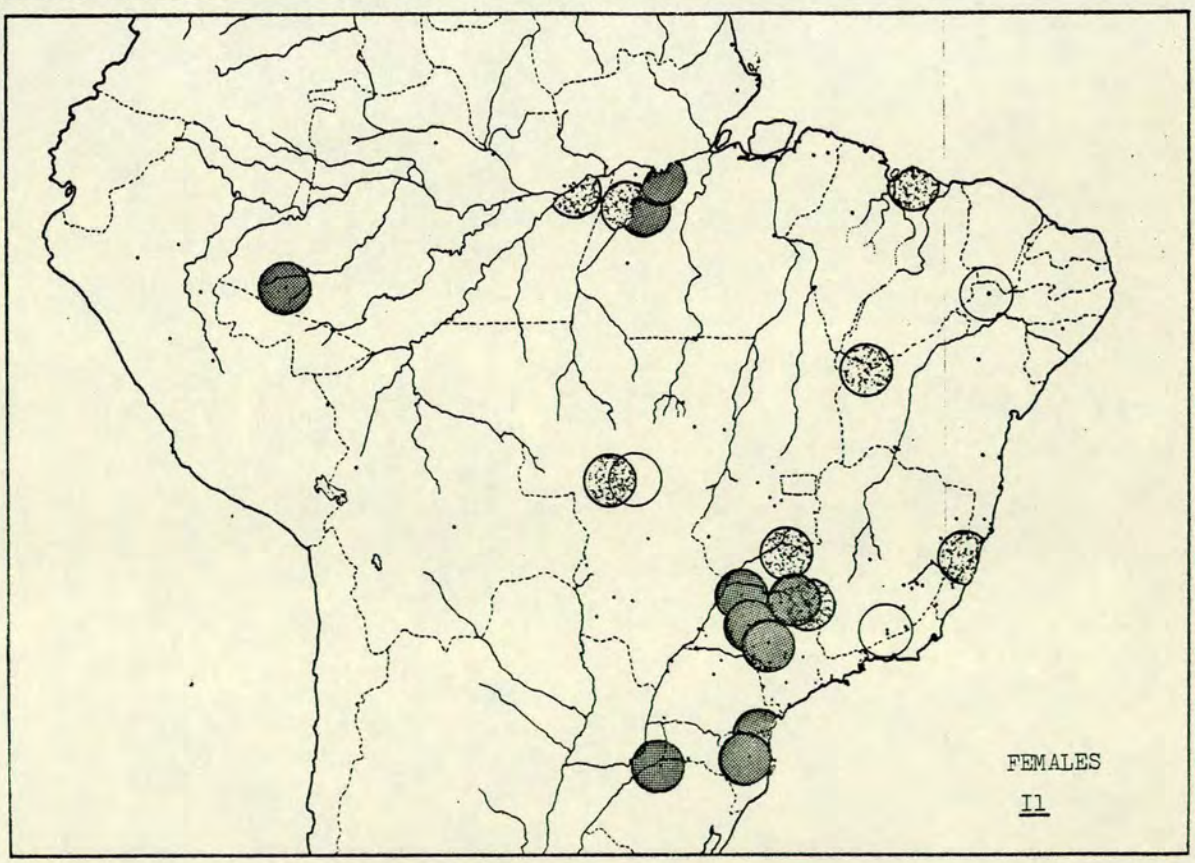
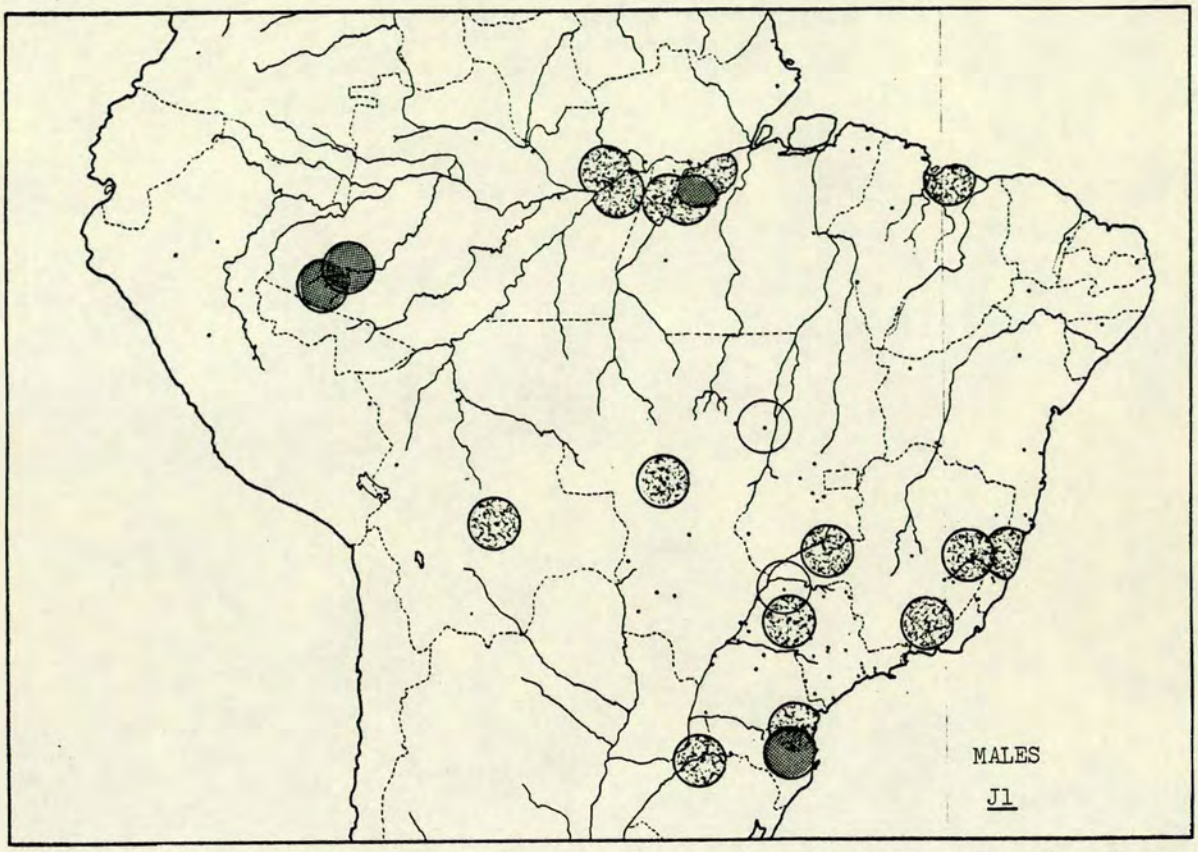

FEMALES
I1

Fig.II.9 - Geographical variation of character J1 (zygomatic breadth)

Shading code as in Fig.II.6. Localities as in Fig.II.3. The mean in each locality and the subset they belong to are:

	MALES				FEMALES			
LOCAL.	MEAN	SUBSETS			LOCAL.	MEAN	SUBSETS	
SP27	66.1	|			MT9	56.8	|	
MT6	67.2	|	|		PA13	57.1	|	|
MG4	68.5	|	|	|	MT13	58.6	|	|
SP13	68.5	|	|	|	BA4	58.9	|	|
MA1	68.9	|	|	|	PA25	58.9	|	|
PA13	68.9	|	|	|	PE1	59.2	|	|
PA25	69.4	|	|	|	MA1	59.3	|	|
AM2	70.0	|	|	|	AM5	59.9	|	|
AM5	70.1	|	|	|	MG13	60.0	|	|
SP22	70.2	|	|	|	RS1	60.3	|	|
MG11	70.2	|	|	|	SP27	60.3	|	|
BOL-2	70.4	|	|	|	SP3	60.4	|	|
MG13	70.7	|	|	|	SP22	60.4		|
SC1	70.9	|	|	|	SP13	60.8		|
MT13	71.3	|	|	|	PA12	60.8		|
PA12	71.9	|	|	|	MG11	62.0		|
RS1	72.3	|	|	|	SC6	62.1		|
ES2	72.4	|	|	|	ES2	62.2		|
PA8	73.4		|	|	SP6	62.2		|
AM6	73.5		|	|	SC1	62.6		|
SC6	75.0		|	|	AM6	65.3		|
AM1	77.0			|				


MALES
J1

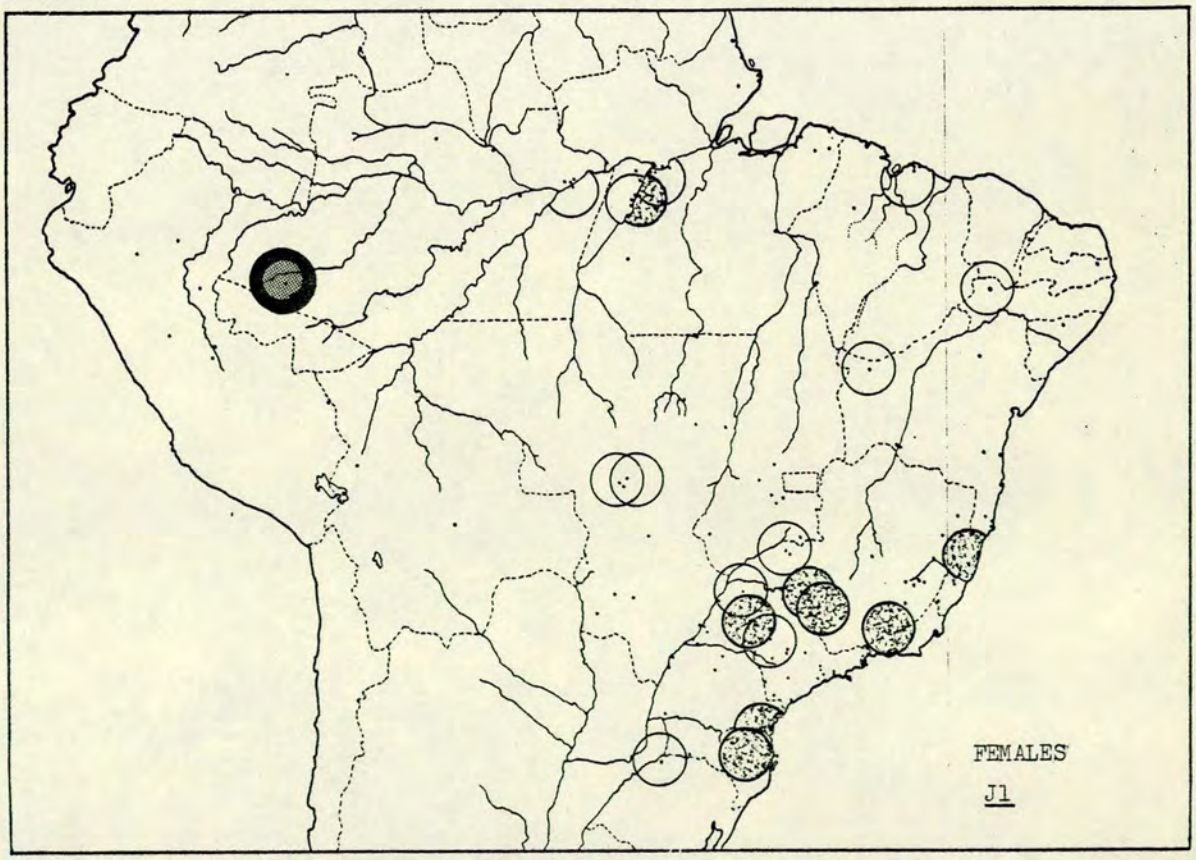
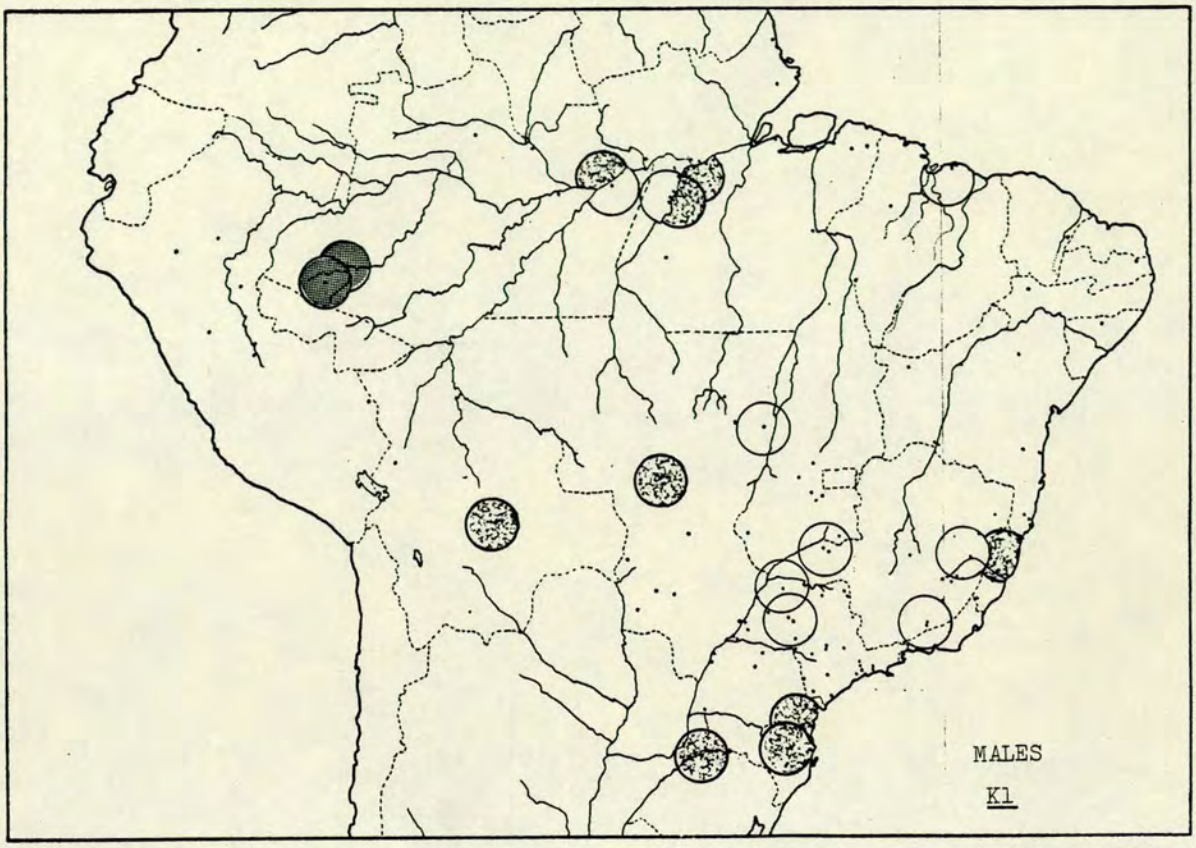

FEMALES
J1

Fig.II.10 - Geographical variation of character K1 (orbital breadth) Shading code as in Fig.II.6. Localities as in Fig.II.3. The means in each locality and the subsets they belong to are:

	MALES			FEMALES		
LOCAL.	MEAN	SUBSETS	LOCAL.	MEAN	SUBSETS
SP27	51.2		PA13	47.4	
MT6	51.4		MA1	47.8	
MG11	52.1		SP22	48.1	
PA13	52.2		SP27	48.1	
SP13	52.3		RS1	48.1	
MA1	52.4		SP3	48.3	
AM5	52.9		BA4	48.4	
MG4	53.0		MG13	48.5	
MG13	53.3		MT9	48.5	
AM2	53.6		PE1	48.6	
MT13	53.6		SC6	49.2	
PA25	53.9		AM5	49.3	
RS1	54.0		PA25	49.4	
BOL-2	54.1		ES2	49.6	
PA8	54.6		MG11	49.7	
ES2	54.7		SP13	49.9	
SC1	54.8		SC1	50.2	
PA12	54.8		SP6	50.2	
SC6	55.2		MT13	50.4	
SP22	55.4		PA12	50.8	
AM6	56.4		AM6	54.0	
AM1	58.5				


MALES
K1

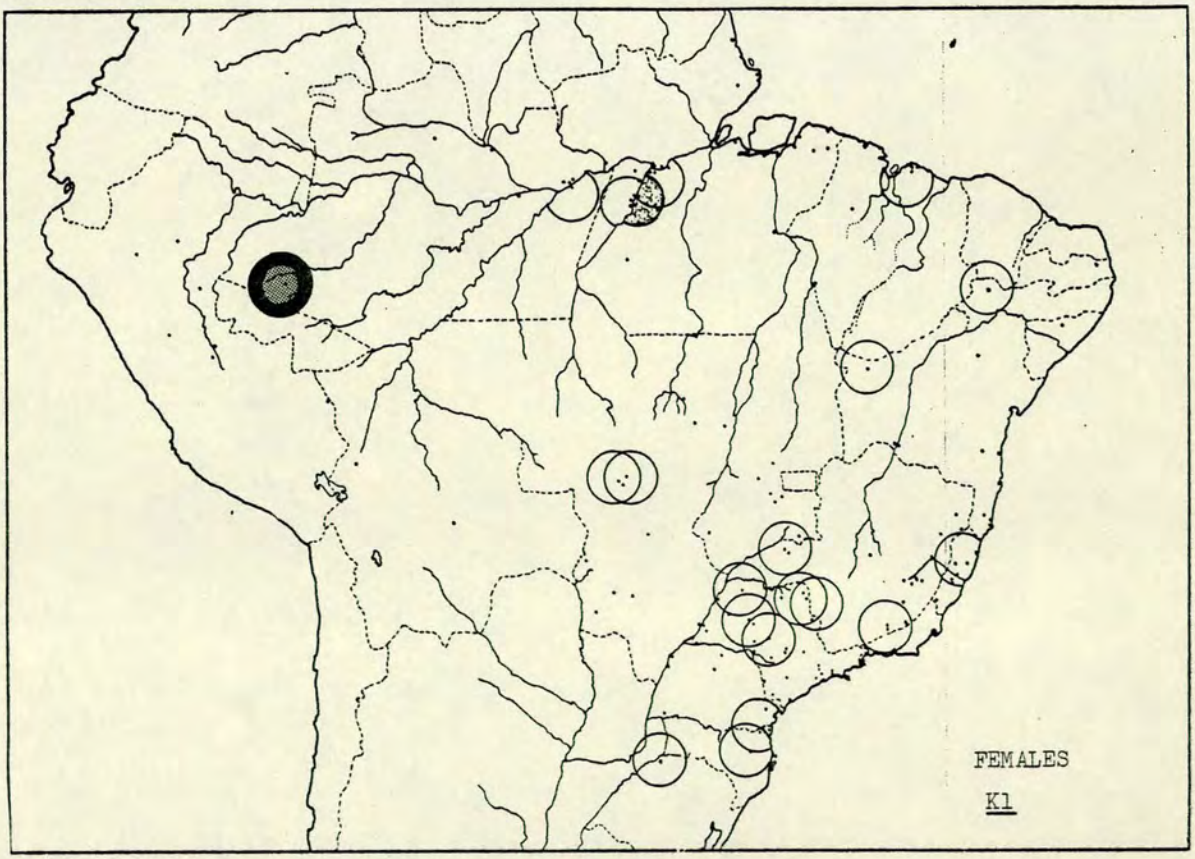
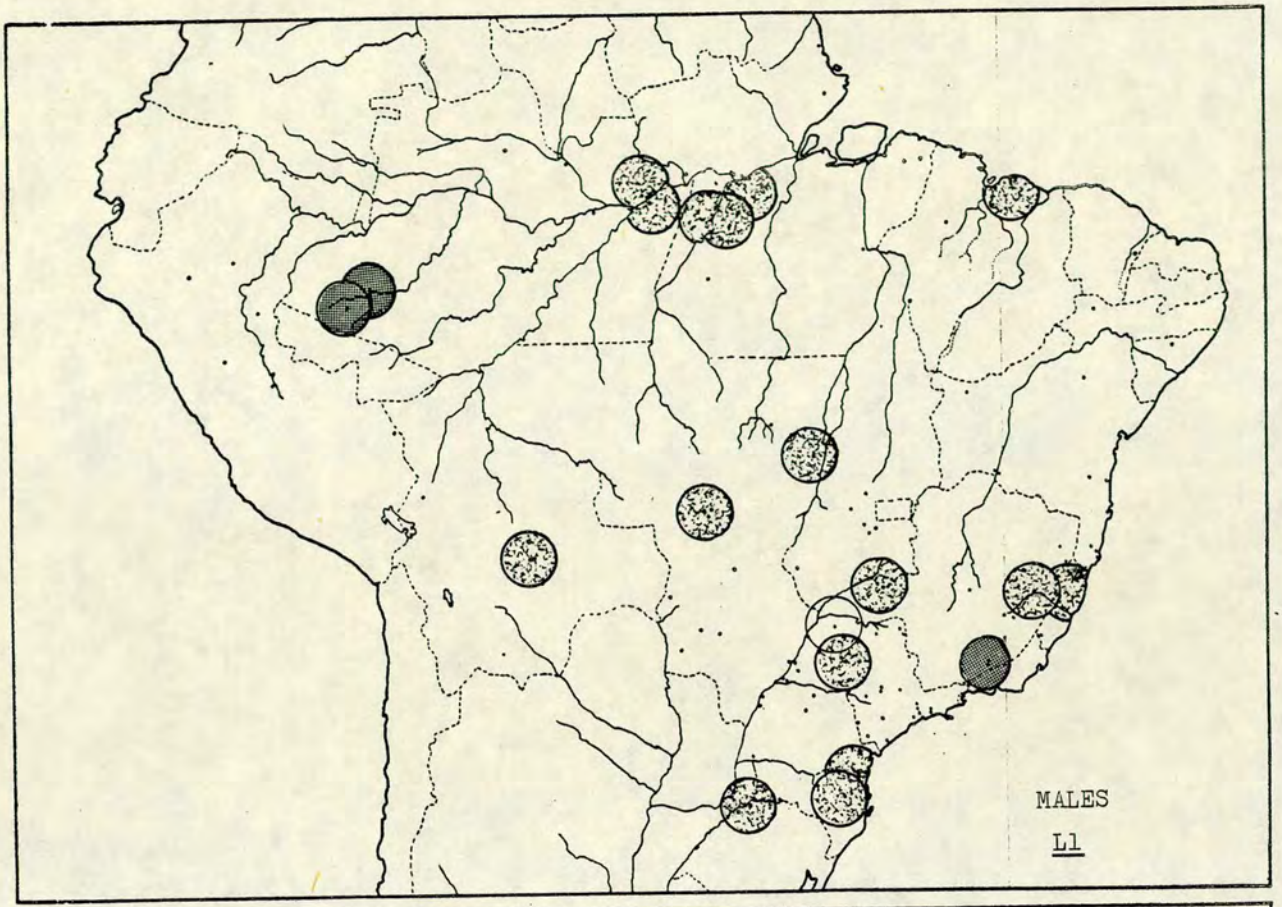

FEMALES
K1

Fig.II.11 - Geographical variation of character L1 (coronoidal height)

Shading code as in Fig.II.6. Localities as in Fig.II.3. The means in each locality and the subset they belong to are:

MALES			FEMALES		
LOCAL.	MEAN	SUBSETS	LOCAL.	MEAN	SUBSETS
SP27	39.2		MT9	32.7	
MG4	39.9		PA13	33.7	
MT13	41.1		PA25	34.1	
PA13	41.2		MT13	34.5	
PA25	41.3		SP27	35.1	
MT6	41.4		SP3	35.2	
SP13	41.4		RS1	35.2	
AM5	41.5		AM5	35.7	
PA12	42.4		SC6	36.0	
AM2	42.5		SP6	36.5	
ES2	43.0		MG13	36.5	
SC1	43.1		PA12	36.5	
MG13	43.5		SP22	37.1	
BOL-2	43.6		SP13	37.3	
PA8	43.9		SC1	37.4	
SP22	43.9		BA4	37.6	
MA1	44.3		MA1	37.7	
SC6	44.5		PE1	38.6	
RS1	45.0		ES2	38.6	
AM6	45.3		MG11	40.4	
MG11	45.7		AM6	41.1	
AM1	47.0				


MALES
L1

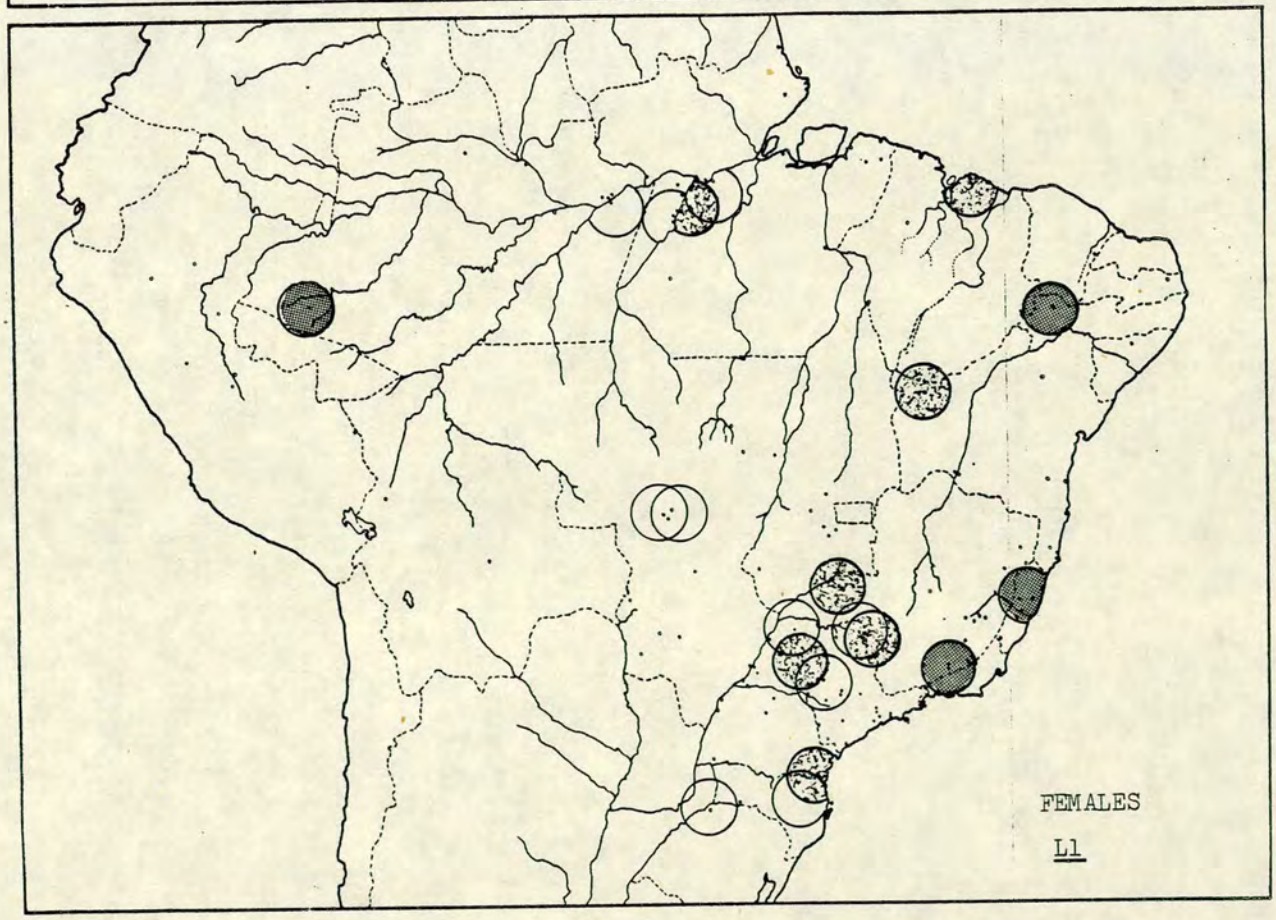
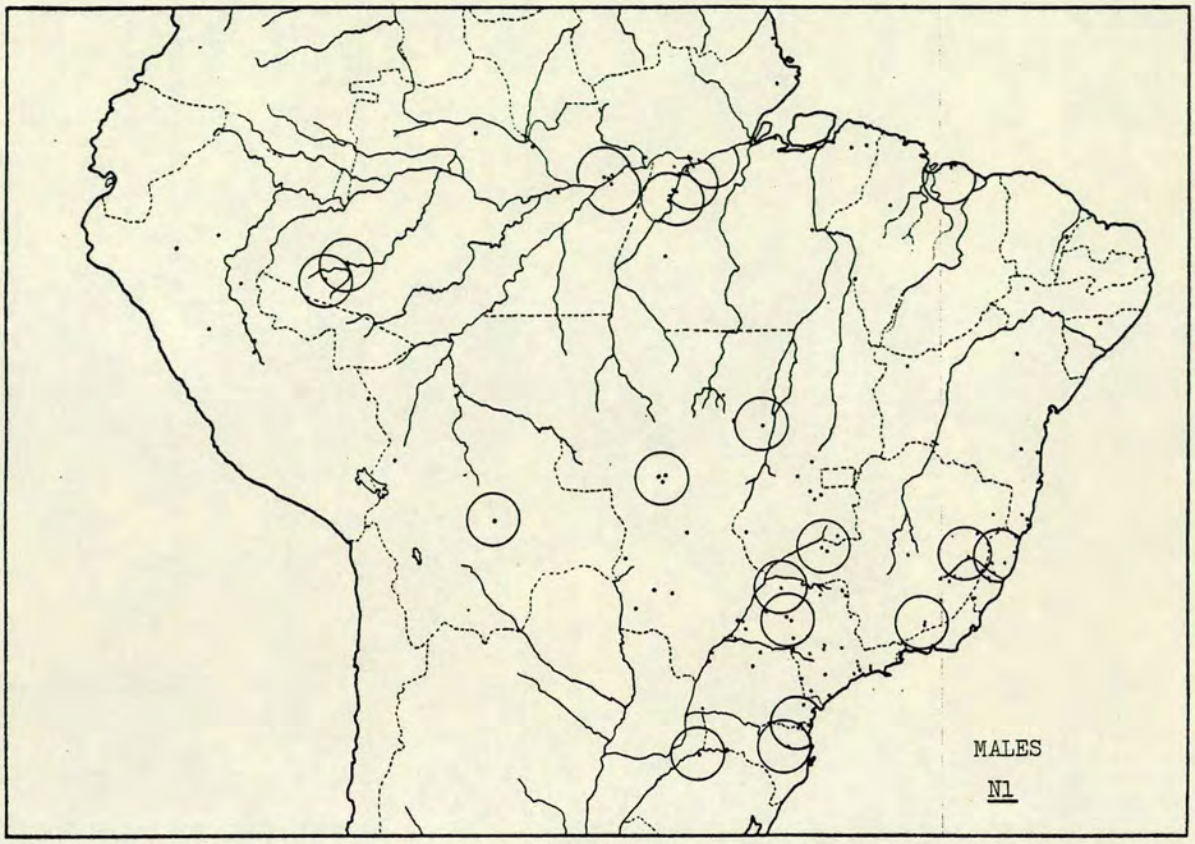
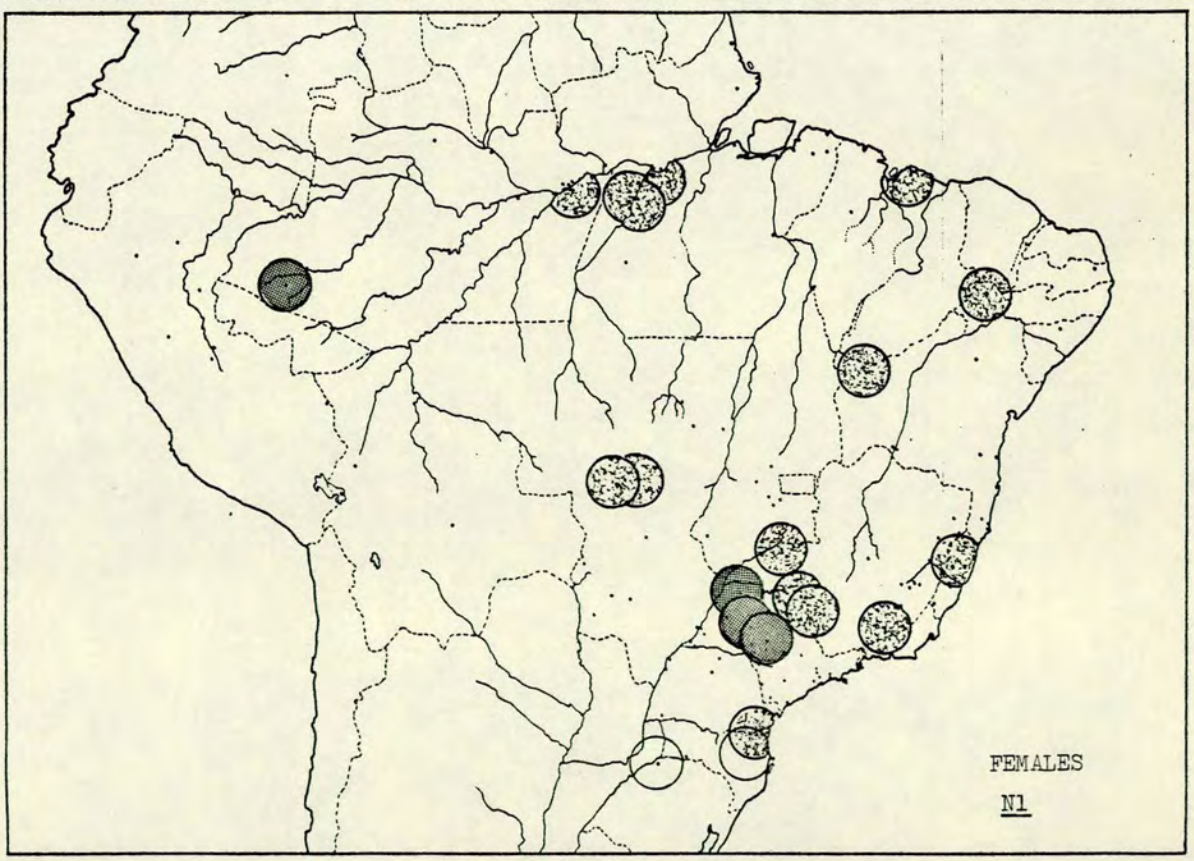

FEMALES
L1

Fig.II.12 - Geographical variation of character N1 (canine length) Shading code in Fig.II.6. Localities as in Fig.II.3. The mean in each locality and the subsets they belong to are:

MALES			FEMALES		
LOCAL.	MEAN	SUBSETS	LOCAL.	MEAN	SUBSETS
SC6	16.0	|	RS1	10.2	|
MT6	16.1	|	SC6	10.3	| |
MG11	16.3	|	MT9	10.6	| | |
MA1	16.4	|	BA4	10.6	| | |
PA12	16.5	|	MA1	10.7	| | |
PA13	16.5	|	PE1	10.7	| | |
SP13	16.6	|	PA13	10.7	| | |
MT13	16.7	|	MT13	10.7	| | |
AM2	16.9	|	PA25	10.8	| | |
BOL-2	16.9	|	MG11	10.8	| | |
RS1	16.9	|	ES2	11.0	| | |
PA25	17.0	|	SP6	11.0	| | |
SP22	17.0	|	SC1	11.1	| | |
ES2	17.3	|	AM5	11.2	| | |
MG13	17.3	|	SP22	11.2	| | |
AM5	17.4	|	PA12	11.3	| | |
SP27	17.8	|	MG13	11.3	| | |
PA8	17.9	|	SP27	11.4	| | |
MG4	18.0	|	SP13	11.4	| | |
AM1	18.6	|	SP3	11.7	| | |
AM6	18.7	|	AM6	12.0	| | |


MALES
N1


FEMALES
N1

to large unsampled areas was risky and might indicate false patterns. I analysed the results in two ways:

(A) categorization of localities according to the general magnitude of the characters' means.

To do this a crude method was used. Values from 0 to 4 were ascribed to each character in each locality according to whether the character mean

0 - belonged to a subset of low means which did not overlap with other subsets

1 - belonged to a group of low means

2 - belonged to a group of intermediate means

3 - belonged to a group of high means

4 - belonged to a subset of high means which did not overlap with other subsets.

The scores were then added up for each locality. The justification for this method is that Figs.II.7 to II.12 indicated the same patterns were repetitive across characters; in some localities most characters had low means, in others most characters had high means. The adding up of scores is a rough way of summarizing the information.

(B) identification of sets of neighbouring localities where several characters have the same magnitude. To do this, I picked any two contiguous localities and checked whether the shading around them was of the same type (i.e. whether the means in both localities had the same general magnitude) in at least half of the characters. If

yes, these two localities were seen as a group; the nearest locality was then added to this group and again I checked whether the three localities had the same shading in at least half of the characters. The "nearest contiguous locality" could be at any distance. There was generally no doubt about whether a sample should or not be considered contiguous, but in the doubtful cases I used Gabriel and Sokal's (1969) practical definition of contiguity.

The procedure above was repeated until the addition of any other locality resulted in the group not being homogeneous in half of the characters. Each locality which had caused a break was then used as the starting point for a new group; their neighbours (including those belonging to previously defined groups) were tested for concordance in mean magnitude. This allows for new groups to partially overlap with previously defined ones. These groups are similar to the "maximal acceptable connected sets" of Gabriel and Sokal (1969).

Higher concordance among localities presumably indicates higher similarity among their populations. If the coverage was good and the races quite distinct in skull size, this system would identify areas of homogeneity and higher similarity. With few samples, the results are more limited.

Results are shown in the form of maps (Fig.II.13) where the "maximal acceptable connected sets" are encircled by different types of lines, according to the similarity level of the group.

Let us consider first the results of procedure A (Figs.II.7 to II.12). The mean values indicated in the caption of these figures was rounded to the nearest 0.1mm. The calculations used more

decimals, allowing for the ordering indicated in the captions.

For each character the S.N.K. tests provided a geographical pattern of size differences. However, these patterns have to be considered with care for several reasons:

- small sample size. The minimum sample size accepted in this study was 4 adult skulls of the same sex. In samples of this size, unrepresentative means are unlikely to appear. Their inclusion in the S.N.K. sequence may confuse an existing pattern or suggest a false one.

- unequal variance. The S.N.K. tests are based on the assumption of equal variance among localities (Sokal and Rinkel 1963, p.483). It is true that the variances do not drift too much; only in 6% of the cases they are either significantly above or below the character average (see Fig.II.18). However, as the variance is not fixed, the distinction of subsets may be in some cases artificial. This difficulty is partly avoided by grouping the means into broader groups ("high", "intermediate" and "low", see Fig.II.6), so that the subsets are not used individually.

- unequal distribution of samples in the studied area. A region that includes many samples is likely to contain at least some discrepant ones. This may give the impression that such area is more heterogeneous than a poorly sampled where, by chance, the few samples fell within the same group. Clearly, since there is more information for the first area, the pattern it reveals, even if not neat, is more reliable than the one observed in a poorly sampled area. In this study, areas like southeastern Brazil and eastern Amazonia are disproportionaly better sampled than, for instance, central Amazonia or central Brazil.

A brief examination of figs. II.7 to II.12 reveals that the picture changes from character to character and that, even within characters, the picture given by males does not match the one given by females. Nevertheless, and in spite of the drawbacks mentioned above, two trends can be found in most of the S.N.K. results:

- in western Amazonia (samples AM1, AM6), most characters have means belonging to the "high" group. In some cases the means are so high as to constitute a subset significantly above all other samples.
- in central Brazil (e.g. samples MT13, MT6), most characters have means belonging to the "low" group. There are however no cases of means so low as to constitute subsets significantly below all other samples.

If we look at the sum of relative scores of each locality (table II.7), the results seem more coherent than in the pictorial form of figs.II.7 to II.12. The sexes give similar results. The two trends suggested by the figures are confirmed, and others are suggested. For instance, localities MT9, MA1, SP27, MG13 and PA13 also have relatively low scores. These localities, and also MT6 and MT13, although quite distant from each other, are all adjacent and can be tentatively grouped as having a common character.

Reasonably high scores are also found in the samples from SC1, in the sample from Bolivia, and also in some samples of R.Tapajós (PA13, PA12). The relatively high values at PA and Bolivia can be a cline towards neighbouring forms, but this does not seem to be the case for SC1, since this locality is near the southern limit of distribution. It seems therefore that the area around SC1 is occupied by a distinct local form.

TABLE II.7

MAGNITUDE OF EACH CHARACTER MEAN IN EACH MAJOR SAMPLE

1 - mean belongs to the group of low means
2 - mean belongs to the group of intermediate means
3 - mean belongs to the group of high means
4 - mean belongs to a subset of high means which does not overlap with other subsets

MALES

Locality	G1	I1	J1	K1	L1	N1	Total
AM1	3	3	3	3	3	1	16
AM6	3	2	3	3	3	1	15
AM5	1	3	2	1	2	1	10
AM2	2	2	2	2	2	1	11
PA13	1	2	2	1	2	1	9
PA12	1	2	2	2	2	1	10
PA4	1	3	2	2	2	1	11
PA8	2	3	3	2	2	1	13
MA1	1	1	2	1	2	1	8
BOL-2	2	3	2	2	2	1	12
MT6	1	1	1	1	2	1	7
MT13	1	1	2	2	2	1	9
MG13	1	2	2	1	2	1	9
SP27	1	2	1	1	1	1	7
SP13	2	3	2	1	2	1	11
MG4	2	2	2	1	2	1	10
ES2	2	2	2	2	2	1	11
MG11	2	1	2	1	3	1	10
SC1	3	3	2	2	2	1	13
SC6	3	3	3	2	2	1	14
RS1	3	3	2	2	2	1	13

FEMALES

Locality	G1	I1	J1	K1	L1	N1	Total
AM1	3	3	4	4	3	3	20
AM5	1	2	1	1	1	2	8
MA1	1	2	1	1	2	2	9
PE1	1	1	1	1	3	2	9
BA4	1	2	1	1	2	2	9
PA13	1	2	1	1	1	2	8
PA12	1	3	2	2	2	2	12
PA4	1	3	1	1	1	2	9
MT9	1	2	1	1	1	2	8
MT13	1	1	1	1	1	2	7
MG13	1	2	1	1	2	2	9
ES2	3	2	2	1	3	2	13
MG11	2	1	2	1	3	2	11
SP27	2	3	1	1	1	3	11
SP22	2	3	2	1	1	2	11
SP6	1	2	2	1	2	2	10
SP13	3	3	2	1	2	3	14
SP3	2	3	1	1	1	3	11
SC1	3	3	2	1	2	2	13
SC6	3	3	2	1	1	1	11
RS1	2	3	1	1	1	1	9

Having detected areas where the means are generally high and others where they are generally low, is it possible to determine the limits of these areas? I tried to do this by identifying the largest areas within which most characters had means of the same magnitude. The method is explained under (b) above, and the results are shown in Fig.II.13. In this figure the results for males look different from those for females. This was partly to be expected because

- the shape of the areas of higher affinity depends on the location of the samples and these differed slightly for males and females; - the average variance is larger in males than in females (see fig.II.18).Therefore, a smaller number of subsets will be distinguished for males by the S.N.K. procedure. The smaller the number of subsets, the smaller the probability that the means belong to groups of different magnitudes. It is therefore not surprising to find that areas of comparable affinity are larger for males than for females.

Although the pictures for males and females look different, the limits of the areas of high and low means are not contradictory in the two maps:

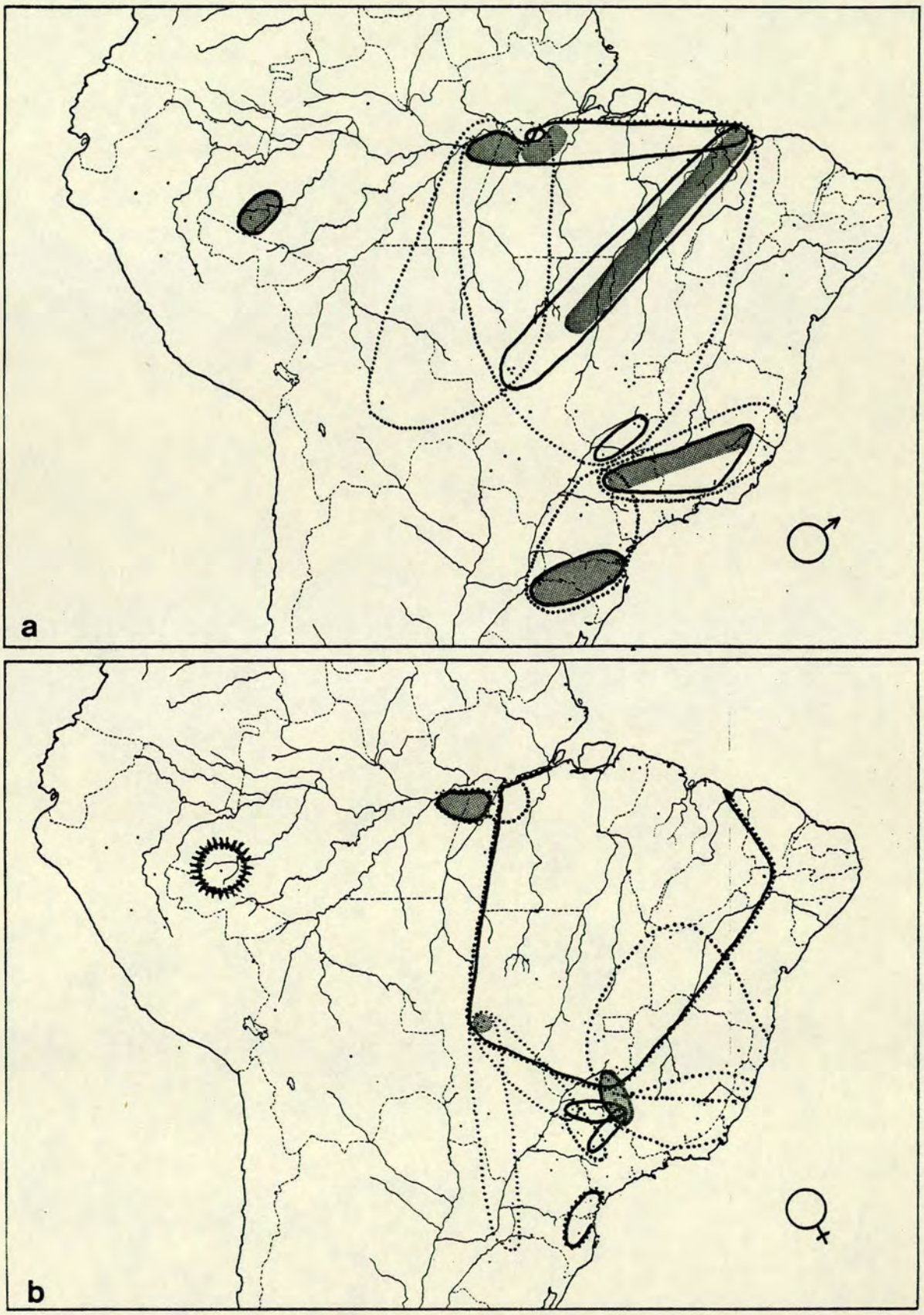
- between localities AM1 and AM6 (where high means were found) there is strong affinity, but this affinity does not extend to the neighbouring samples (which are, however, quite far from AM1 and AM6). These two samples seem to constitute a very distinct, isolated group.

- among the localities with low means there is also some affinity. In contrast to the previous case, the area which contains these related localities is quite large. Some of the localities involved

Fig.II.13 - Maximal acceptable connected sets

Dotted lines encircle the largest groups of neighbouring localities where same category (low, high or intermediate) as defined in Fig.II.6. A thick line is used when the means of at least 4 characters (66.6%) of all enclosed localities belong to the same category. Shaded areas include the localities whose samples were concordant in 5 characters (83.3%). A barbed line is used in the one case where the locality was always of a diferent category from the neighbouring localities.

Map a - males; map b - females.


a
♂
b
♀

also belong to other sets of related localities. For instance, animals from the lower Amazon also have some affinity with Bolivian animals; animals from MT (central Brazil) also have some affinity with those from southern and southeastern Brazil. In eastern Brazil, the animals from BA also have affinities with those from ES and eastern MG.

- animals from SC had relatively high mean values. There seems to be a great affinity among samples SC1, SC6 and RS1. They also have some affinity with samples from SP.

How reliable are these outlines of related localities? When one deals with races, it is to be expected that, if there are no present barriers, each will intergrade with the neighbouring ones, and that some sets of related localities will overlap with others. Areas where races are not mixed should appear as areas of high affinity. However, this can only show if there is an homogeneous distribution of samples over the whole area of distribution (which is not the case in this study) and if all means are representative. Also, some areas may look homogeneous only because they are poorly sampled. They could be harbouring unsampled populations of distinct races.

Since only a few characters were used, the samples were small and the distance between samples quite large, it is unlikely that the pattern shown in Fig.II.13 is reflecting the real shape of the areas of comparable similarity. Therefore this pattern should not be used as a firm base for race separation. It can, however, be used to check the pattern suggested by the other characters.

Do the coefficients of variance indicate any geographical pattern?

The mean C.V.s (skull morphometric characters) are generally under 5%, which is an acceptable level of variation. As these C.V. were calculated from samples of different sizes, they are not equally representative. Particularly high or particularly low values of C.V. were found in 6% of the cases. Fig. II.18 shows their distribution. I had expected that some areas (of secondary contact between races) would include larger C.V. than others, but I failed to detect any pattern in this figure.

Quantitative characters (considered together)

In the procedure above the size differences were investigated with univariate methods, which strictly do not indicate affinities between units (units could be either individuals or populations). Such affinity can be investigated through a multivariate analysis. There are various multivariate techniques; as each gives only an approximate assessment of affinities, Thorpe (1976, p.446) recommends that one should make several analyses, varying methods and character sets, to estimate the consistency of the results obtained. I used a multivariate approach to group individuals according to their similarity in skull morphometric characters and then compared the groups thus defined with those suggested by the qualitative characters. The discrimination of groups was done by cluster analysis, using CLUSTAN (Cluster Analysis Package) (Wishart 1982) in the Edinburgh Regional Computer Center ICL 2972 computer. This treatment requires that there are no missing values in any specimen. Thus, if a skull had a broken part (e.g. upper canines

missing, broken zygomatic arch), the specimen has to be excluded from analysis. This restricted my sample to circa 130 adult specimens of each sex. As a first step the variables were substituted by a smaller number of composite variables or principal components (CLUSTAN procedure FILE); principal components can often be interpreted in biological terms. Such reduction is performed on the belief that the correlations between variables are the result of some underlying regularity which might be affecting different variables in different ways. Each component is defined in such a way that they may be said to explain part of the data variance. In the present case most of the variance was explained by the first three components, as shown below:

Percentage of variance explained by the first three factors (*)

	Factor I	Factor II	Factor III	Cumulative
MALES	61.2	13.2	10.4	84.8
FEMALES	54.8	13.3	12.7	80.8

(*)- Principal component analysis and factor analysis are often referred to as being identical. Although they may provide similar results, there is an important distinction between them; factor analysis assumes a definite mathematical model (uncorrelatedness of residuals) whereas principal component does not (Marriott 1974). Thorpe (1976) also indicates that these analyses are different and mentions the general inferiority of F.A. as compared to P.C.A. for the majority of purposes. In this study I used CLUSTAN procedure FILE; although the CLUSTAN manual indicates that a P.C.A. is performed, in its output the term "factor" is used. I have also used the terms "factor" and "component" interchangeably.

The factor loadings of each character are shown in table II.8. As the loadings are similar in the two sexes, the same factor interpretation holds for both males and females. The first factor, which involves more than 50% of the variance, seems to be equally affected by G1,H1,J1,K1 and L1. It can be seen as an overall size factor. I1 and N1 are less related to factor I, but are, respectively, the main determinants of factors II and III.

Fig. II.14 shows the average factor scores of each sample (each dot is the average of individual factor scores in that locality) for the first three vectors. This scattergram is not particularly revealing. There is no obvious tendency for the averages to be aggregated into isolated and geographically meaningful clusters. Individuals from AM1 (males) and from AM6 (females) have obviously much larger scores on factor 1 than individuals from other localities, and it is also clear that individuals from MT6 (males) and and MT9 (females) have very large negative scores on the same factor; however, the general aspect is that of an indistinct mass of intermediate scores on both factors (a comparable pattern, showing individuals rather than locality average is presented in Fig.II.16). In this area the only pattern I was able to distinguish is the apparent sharing of low scores on factor 1 by animals from MA1, PE1 (northeast Brazil), MT9 and MT6; however, this could have been due to small sample sizes. In general, the plotting of factor scores confirms the indications of the univariate analysis, but does not provide a much better discrimination of groups. This is probably because most of the variance is associated with factor I, the size factor, and size differences can be adequately identified through the univariate S.N.K. tests.

TABLE II.8
FACTOR LOADINGS ON EACH CHARACTER

Only the first three components are shown. The information is presented in two ways: in a numerical form (left) and with signs (right). The number of signs indicate the magnitude of the factor loading, according to the following code:

0.0 to 0.3 ..... + or -
0.3 to 0.6 ..... ++ or --
0.6 to 0.9 ..... +++ or ---

MALES

Characters	Factors			Factors		
	I	II	III	I	II	III
G1	0.43	-0.02	-0.10	++	-	-
H1	0.45	0.03	-0.05	++	+	-
I1	0.26	0.71	-0.51	+	+++	--
J1	0.43	-0.13	-0.01	++	-	-
K1	0.40	-0.18	-0.12	++	-	-
L1	0.37	-0.50	0.09	++	--	+
N1	0.26	0.45	0.84	+	++	+++

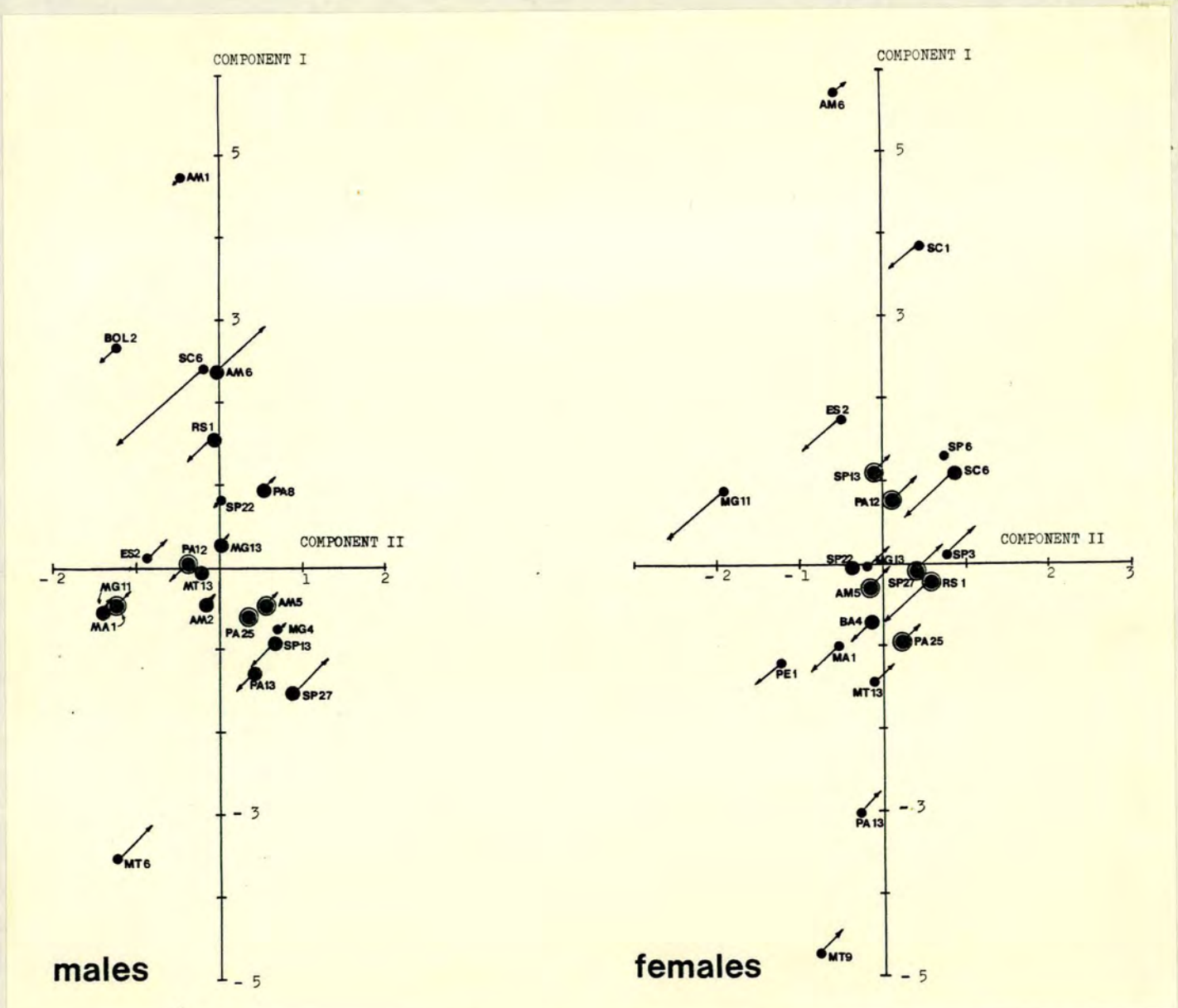
FEMALES

Characters	Factors			Factors		
	I	II	III	I	II	III
G1	0.44	0.16	-0.17	++	+	-
H1	0.46	0.00+	-0.13	++	+	-
I1	0.25	0.82	0.22	+	+++	+
J1	0.47	0.00+	-0.14	++	+	-
K1	0.38	-0.15	0.16	++	-	+
L1	0.36	-0.43	-0.29	++	--	-
N1	0.22	-0.30	0.88	+	--	+++

Fig.II.14 - Principal component analysis

Each point represents one locality, plotted according to its "loading" on the three principal components (this "locality loading" is the mean of the loadings of all individuals of that locality) Loading on component 3 is shown as inclined arrows whose direction represents sign (left negative, right positive) and with length proportional to the loading.

Sample sizes varied from n=2 to n=29. Small dots are used for samples of less than 4 individuals; encircled big dots are used for samples of at least 8 individuals.



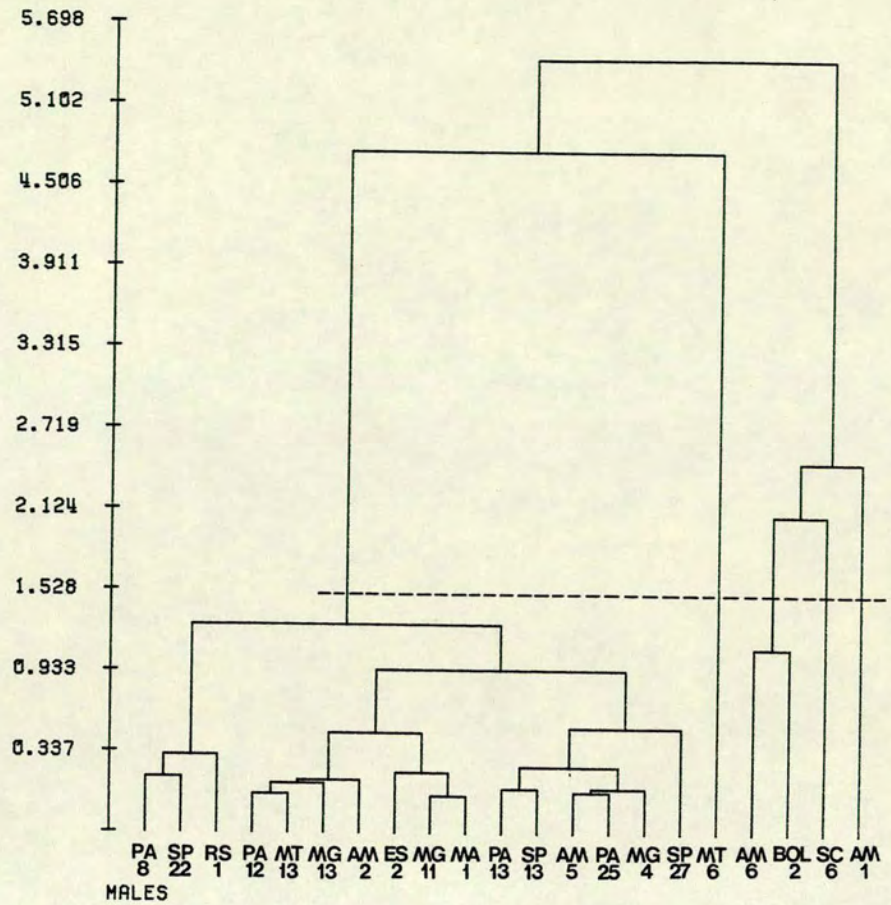
Although the plot does not visually identify groups of related localities, the affinities between populations can be estimated through the relative position of their factor scores when the vectors are plotted one against another to produce a scatter diagram. This is a valid classificatory method (Thorpe 1976, p.434). The affinities between animals of different localities was investigated with the CLUSTAN procedures CORREL, RELOCATE and HIERARCHY. The first one creates a similarity matrix relating each individual to all others on the basis of their factor scores (the similarities were expressed in terms of the squared euclidean distance coefficient, which is in fact a dissimilarity index). RELOCATE then defines the initial set of "clusters", each consisting of all the individuals from a given locality, and calculates the similarity between them. Procedure HIERARCHY then determines the levels of similarity (or dissimilarity) at which the various clusters can be aggregated, starting from the two most similar clusters and progressively adding less similar ones by means of a variable combinatorial transformation of the similarity coefficients.

The results are presented in two ways: Fig. II.15 is a dendrogram showing the linkage between the samples of different localities (obtained with CLUSTAN procedure PLINK), and Fig. II.16 shows a cluster diagram for the level of 5 clusters (indicated in fig. II.15 by dotted line).

The maximum number of clusters is, obviously, the number of localities used in the study. These can, in theory, be aggregated into progressively larger clusters until only one, containing all localities, is recognized, at a high dissimilarity level. The

Fig.II.15 - Dendrograms showing the linkage between the samples of the various localities. Samples on the X-axis are progressively linked at the increasing dissimilarity level indicated on the Y-axis. A - males; B - females

A)


5.698
5.102
4.506
3.911
3.315
2.719
2.124
1.528
0.933
0.337
PA 8
SP 22
RS 1
PA 12
MT 13
MG 13
AM 2
ES 2
MG 11
MA 1
PA 13
SP 13
AM 5
PA 25
MG 4
SP 27
MT 6
AM 6
BOL 2
SC 6
AM 1
MALES

B)

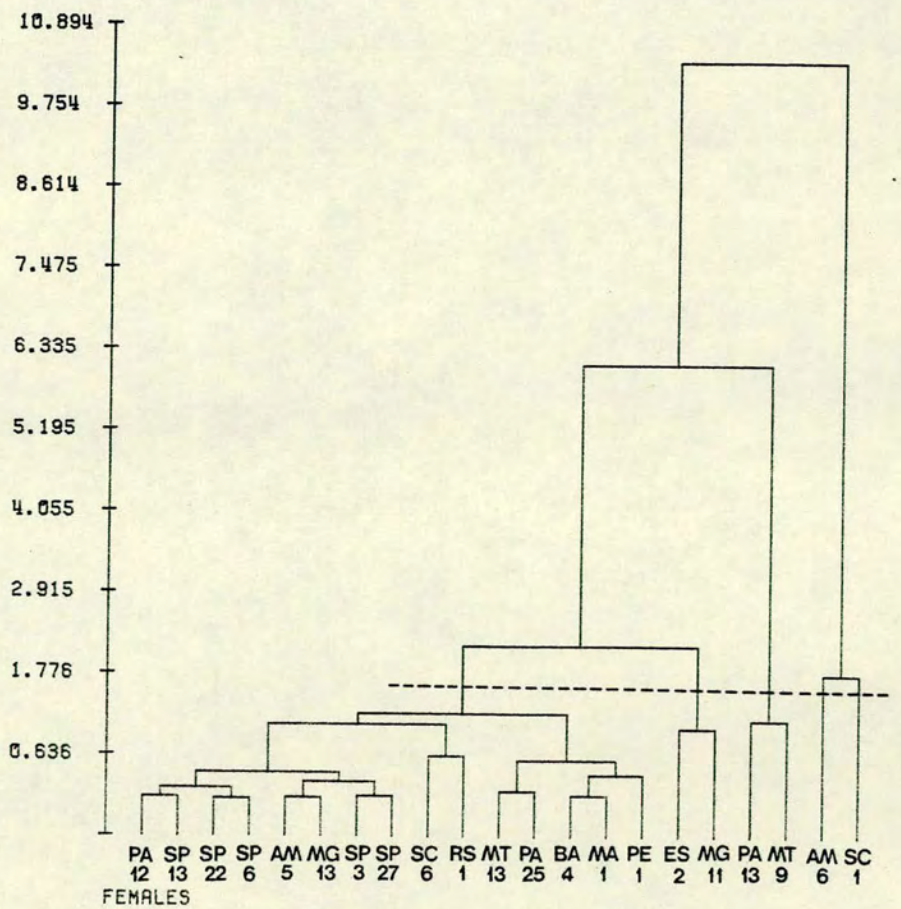
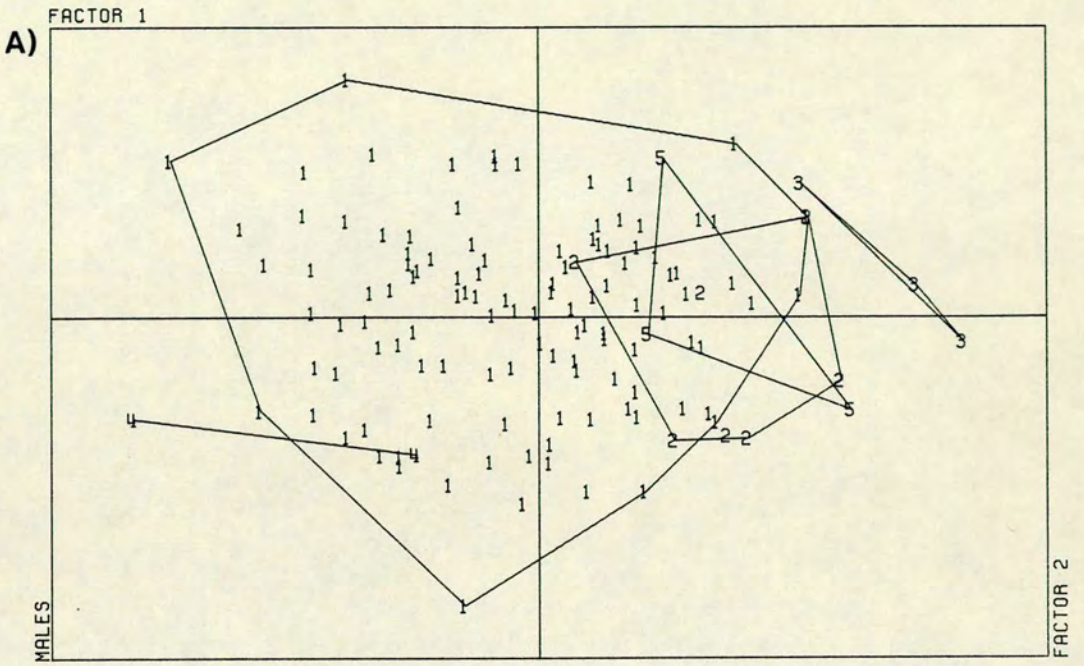

10.894
9.754
8.614
7.475
6.335
5.195
4.055
2.915
1.776
0.636
PA 12
SP 13
SP 22
SP 6
AM 5
MG 13
SP 3
SP 27
SC 6
RS 1
MT 13
PA 25
BA 4
MA 1
PE 1
ES 2
MG 11
PA 13
MT 9
AM 6
SC 1
FEMALES

Fig. II.16 - Scattergram of individual factor scores. Each point is one individual, plotted according to its scores on the first two factors. Each of the five clusters intersected by the dotted line in Fig. II.15 are represented in this figure by polygonal outlines. Each outline encircles the scores of all individuals belonging to that cluster; individuals of other clusters may be within in the polygon in the cases where there is little distinction between clusters.

A) MALES
cluster 2: BOL2 and AM6
cluster 3: AM1
cluster 4: MT6
cluster 5: SC6
cluster 1: all remaining localities

B) FEMALES
cluster 2: MT9 and PA13
cluster 3: AM6
cluster 4: SC1
cluster 5: ES2 and MG11
cluster 1: all remaining localities


A)
FACTOR 1
MALES
FACTOR 2

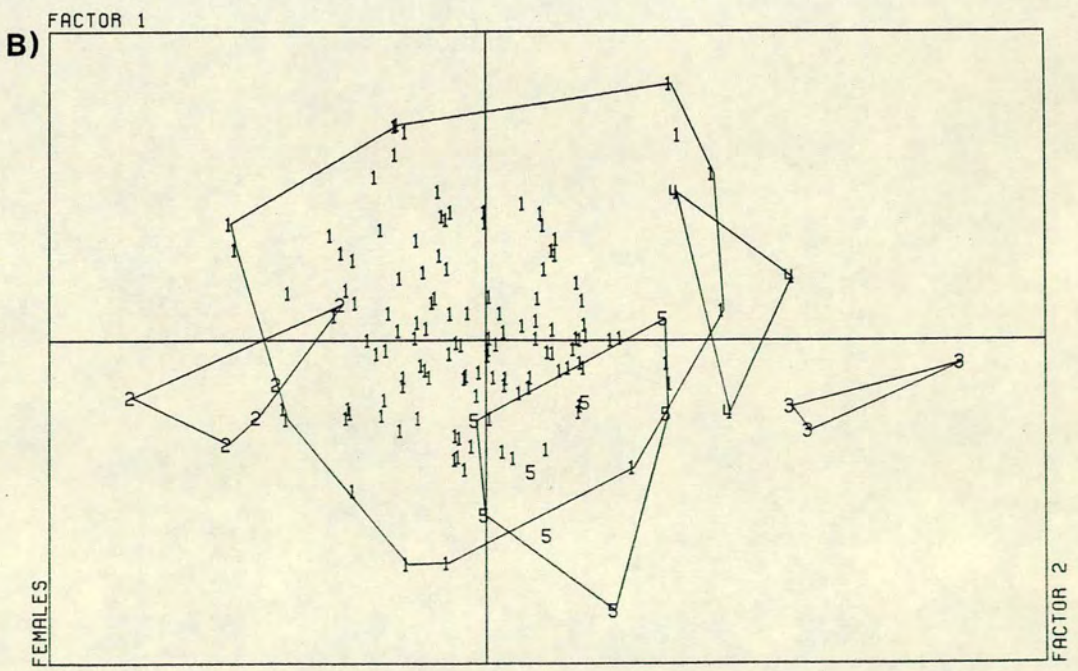
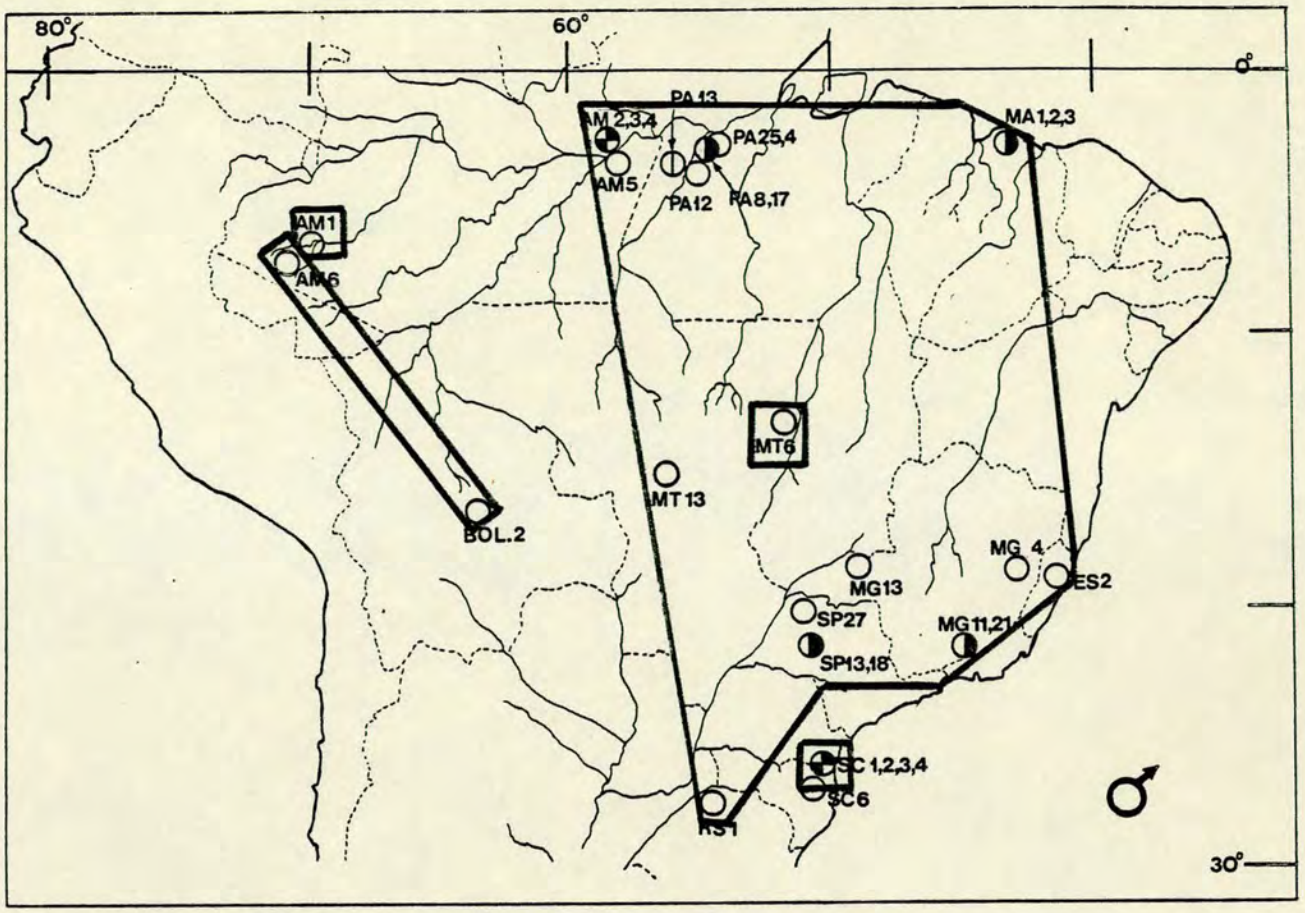
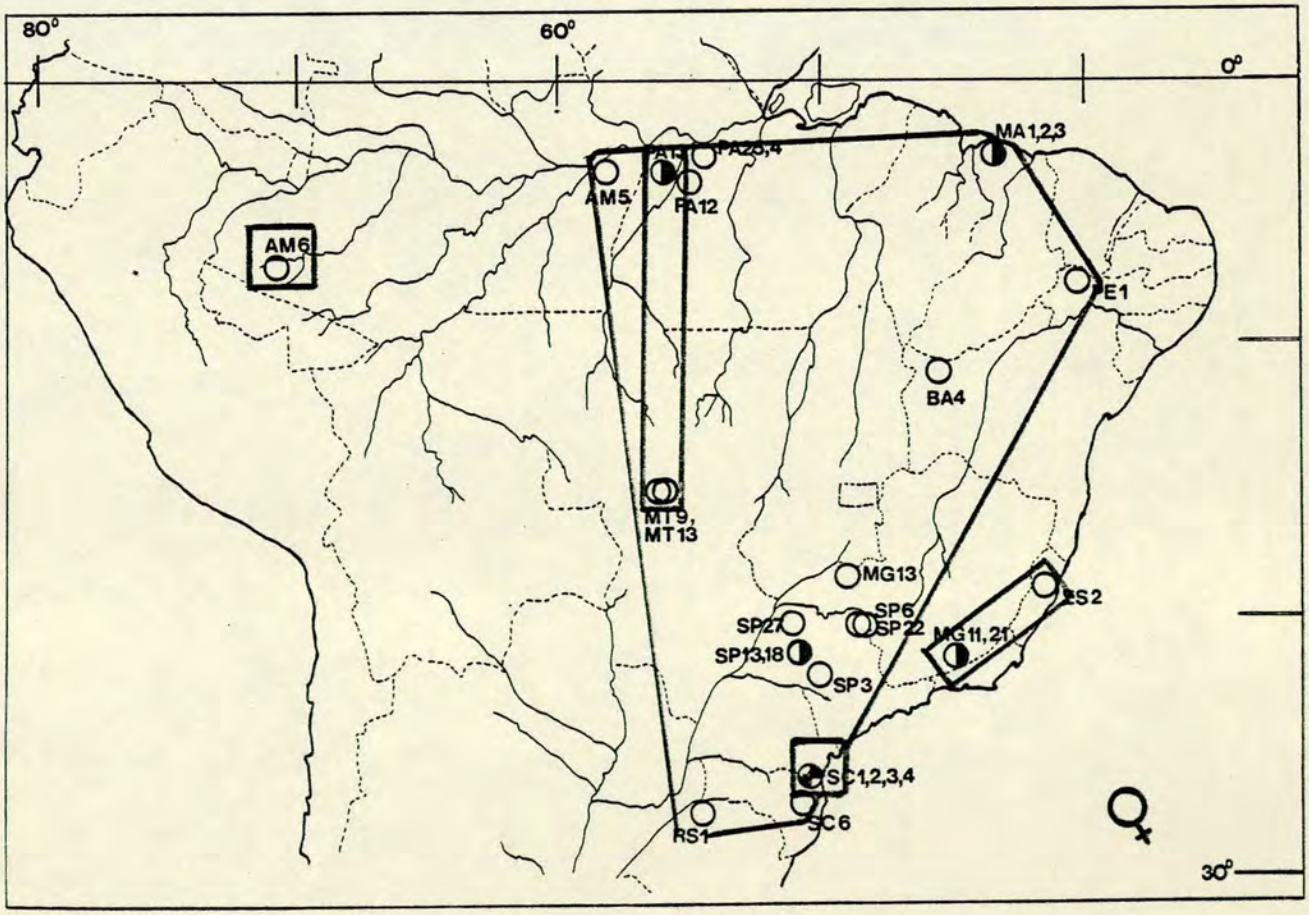

B)
FACTOR 1
FEMALES
FACTOR 2

Fig. II.17 - The geographical representation of the clusters in Figs.II.15 and II.16.


80°
60°
0°
PA13
AM 2,3,4
PA25,4
MA1,2,3
AM5
PA12
PA8,17
AM1
AM6
MT6
MT13
BOL.2
MG 4
ES2
MG13
SP27
MG11,21
SP13,18
SC 1,2,3,4
SC6
RS1
30°


80°
60°
0°
MA1,2,3
AM5
PA12
AM6
E1
BA4
MT9,
MT13
MG13
ES2
SP6
SP27
SP22
MG11, 21
SP13,18
SP3
SC1,2,3,4
SC6
RS1
30°

number of clusters to be accepted as natural groups depends on the level of dissimilarity one is prepared to accept. On the basis of pelage colour at least 5 groups can be readily distinguished; at least 3 of these would be represented in the samples used for the multivariate analysis. Thus, assuming that the skull measurements parallel the differences found in the qualitative characters, not less than 3 clusters should be recognized. Because Fig. II.15 indicates that the acceptance of not more than 4 clusters would require the acceptance of a relatively high dissimilarity coefficient, a minimum of 5 clusters had to be accepted.

Fig. II.15 shows that the clusters, even when considered at high dissimilarity level, often include a single locality. This is either due to the poor geographic coverage of the present sample, or to some races occurring only in very restricted areas. Fig. II.16 shows that there is much overlap between the factor scores from different clusters. This either indicates that the skulls do not reflect racial differences very well or that most samples belonged to intermediate forms. Nevertheless, the patterns that emerge agree both with the indications from the univariate analysis and with the indications from the qualitative data (below); there is a large area including central and northeastern Brazil where animals seem to be more or less indistinguishable from the skull point of view. The clusters indicate the uniqueness of localities from western Amazonia (AM6), southern Brazil (SC1), central Brazil (MT6) and eastern Brazil (ES2,MG11/females). Fig. II.17 represents the 5 clusters of Fig.II.16 on a map.

Semi-qualitative characters

Vomer pneumatisation

Della Serra (1950) observed that in C.albifrons (he called them C.gracilis) the tips of the vomer wings were subdivided, and that this did not happen in the other forms (all C.apella) that he examined. C.capucinus and C.nigrivittatus also have subdivided vomer wings, so this character is a very reliable way of separating tufted from untufted Cebus.

Since this bone is quite plastic, it seemed potentially useful to separate the races of C.apella. However, the mean pneumatization grade did not reveal geographical patterns (Fig.II.19) maybe because most samples were of small size. The only recognizable group is constituted by some localities in southern Brasil (RS1, SC1 and SP12) where grade 3 seems to be rare (see area "A" in fig. II.19).

Other aspects of vomer shape can also be useful. For instance there is a set of contiguous localities (BA2, BA3, ES1, ES2, ES3, MG3), where the vomer wings touch one another only at the anterior end (see area "B" in fig. II.19).

Conspicuousness of the sagittal crest

The height of the sagittal crest was only noted when it was particularly high, and notes were taken about it being very low only when the animal was old and I expected a higher crest. Even with this rather restricted type of information, Fig.II.20 indicates that there are geographical differences in crest conspicuousness, and that this is a useful character. However, there seems to be more than one factor influencing crest development. A crest may be low due either to the tendency of that particular form not to produce large crests, or to their development being slowed or delayed. In

the last case, only old animals would show the full development, and old animals are not numerous in the samples.

A larger sample would probably improve the pattern shown in Fig.II.20. most of the half-covered circles would be probably substituted by triangles or plain circles, and one might draw isophenes based on the % of crested animals. Nevertheless, the data available at the moment allow the distinction of at least three sets of localities:

- an Amazonian group of localities (including the Bolivian one), characterized by poorly developed crests;
- an area near the coast in southeastern Brazil, where crests can be remarkably high (sometimes reaching 8 mm);
- an area including central and northeastern Brazil, where the crests may develop but seem to sometimes have a delayed development.

Qualitative characters

Colour of ventral hairs

I started taking systematic notes on the colour of ventral hairs only after I had already examined part of the available material. As the note-taking was not homogeneous, the analysis of the geographic variation in this character is less reliable. However, I believe that careful notes would not drastically change the results (shown in Fig.II.21). Ventral hairs are variable in colour and almost invariably the hairs have the base with a different colour from the tip, which makes it difficult to decide which is the "general" colour. The categories used in this figure had to be kept very broad and partly overlapping. With a larger sample the categories might be modified: the crosses would be

possibly substituted by one of the other categories and the circles subdivided into more detailed categories (e.g. based on the % of the population with one colour or another). Nevertheless, with the present categories, at least six groups of localities can be identified. The largest one is maybe less homogeneous than it looks, but this cannot be resolved with the present sample.

Cap colour

Because most of the categories of cap colour were very similar and quite likely to be confounded under varying light conditions, I decided to only consider as distinguishable the lighter one ("brown"). See Fig.II.22.

Presence and distinctiveness of a dorsal stripe

The geographical pattern obtained (Fig.II.23) is quite compatible with the ones indicated by other qualitative characters. Again the large area including central and northeastern Brazil appears as an homogeneous set.

Colour of flank hairs

The pattern shown in Fig.II.24 matches very well the picture given by the character colour of ventral hairs. There are three very well defined areas along the Atlantic coast, one on western Amazonia, and one including the lower Amazonas and the French Guiana. Again there is a large area including central and northeastern Brazil characterized by a complex mixture of phenotypes. As a similar trend is revealed by several other characters, it is probable that this area constitutes an authentic

set, not an artifact of the phenotype categorization I used.

Variability in flank colour

In Fig.II.25 I indicated the localities where either the animals flanks have a mottled appearance or where the flank colour is particularly variable. The mottled appearance is frequently due to the tip being of a different colour from the rest of the hair. The isophenes from Fig.II.24 are also reproduced here, and it can be seen that the dots and circles are mostly outside of the areas delimited by the isophenes. This reflects the phenotypic complexity in the large area which includes central and northeastern Brazil. Fig.II.25 also shows the type-localities of several forms of Cebus apella. This information will be used in a comparison between the types and the phenotypes I observed for the area where they were collected.

Cap shape

The largest samples indicated that this character is generally so variable within localities that it is risky to consider a single specimen as representative of any locality. I established that a sample of four adult skins was the minimum for a locality to be considered "well" represented. This is a low minimum but I preferred to lose in accuracy to gain in geographical coverage. After all the phenotypes in these samples had been examined, I tried to detect patterns and to draw isophenes on their distribution map (Fig. II.26). The smaller samples were used to locate the limits of a particular geographical pattern indicated by the "acceptable" samples.

Fig.II.18 - Localities where one or more of the morphometric characters showed particularly high or particularly low coefficients of variation. High C.V. are indicated by circles, low C.V. by diamonds. By "particularly high" it is meant a value that is two standard deviations above the mean C.V. for a given character and a given sex. The average C.V. for each character is:

	MALES	FEMALES
G1	2.3%	2.4%
H1	3.0	2.8
I1	2.8	2.8
J1	4.5	2.5
K1	3.8	3.0
L1	6.2	4.6
N1	5.8	5.7

$$C.V. = \frac{\text{stand.dev.}}{\text{mean}} \times 100$$

The cases included in this figure are:

-- two st.dev. above average: MT13 (G1 males and females, H1 females); BOL2 (L1 males, K1 males); SC1 (L1 females); PA13 (G1 females); MG4 (N1 males); MG13 (G1 males); MT9 (L1 females); SP3 (N1 females); SP6 (I1 females).

-- two st.dev. below average: MG11 (L1 females); MG4 (J1 males); ES2 (H1 males); AM2 (I1 males); AM6 (N1 females); SP22 (N1 males).
The data used for the determination of these C.V. had been previously standardized to age 12, so these C.V. do not include variation due to age.

Fig.II.19 - Mean grade of vomer pneumatization in each major locality.
Within each circle, the top value is the male mean value, the bottom one is the female mean value. Grades were 1,2 and 3 (as defined by Della Serra 1950) or intermediate values between them (1.5, 2.5).

A - localities where pneumatization grade 3 seems to be rare: RS1, SC1, SP12

B - localities where vomer wings only touch one another at the anterior end: BA2, BA3, ES1, ES2, ES3, MG3.

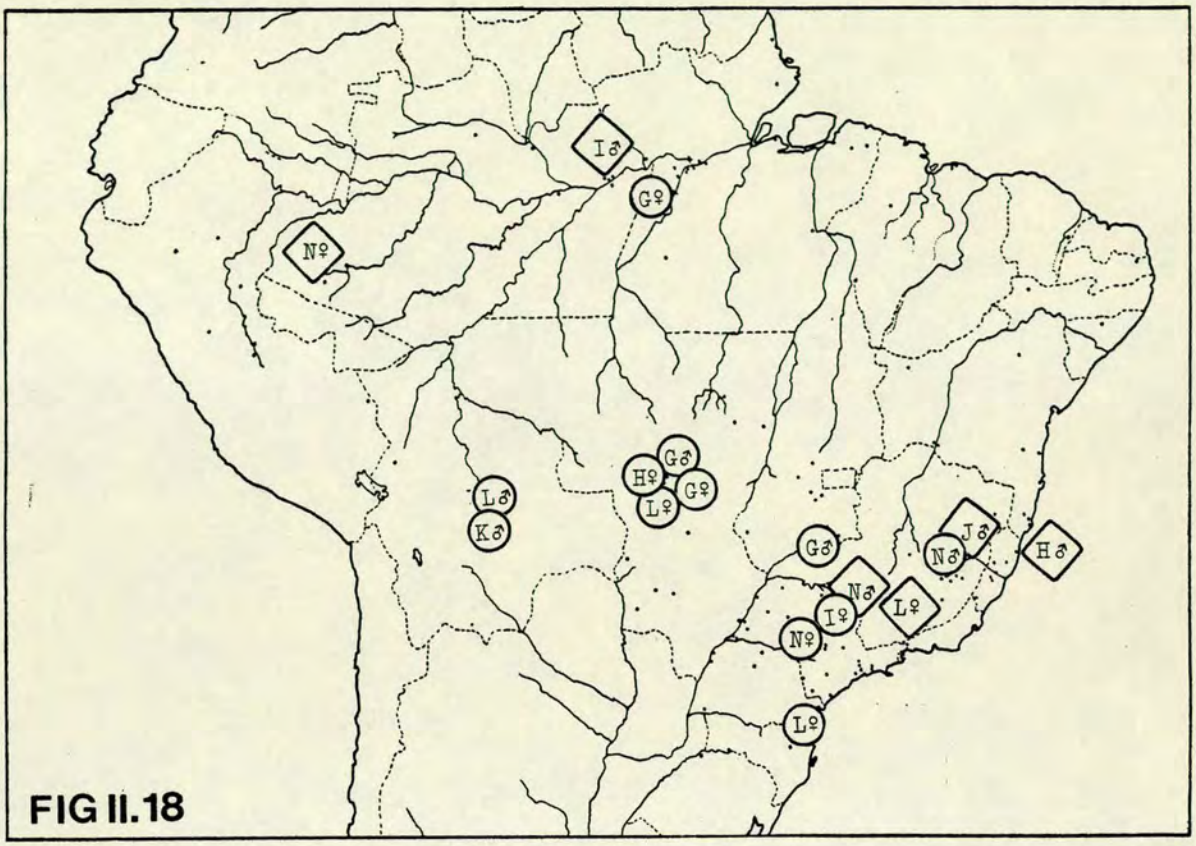


FIG II.18

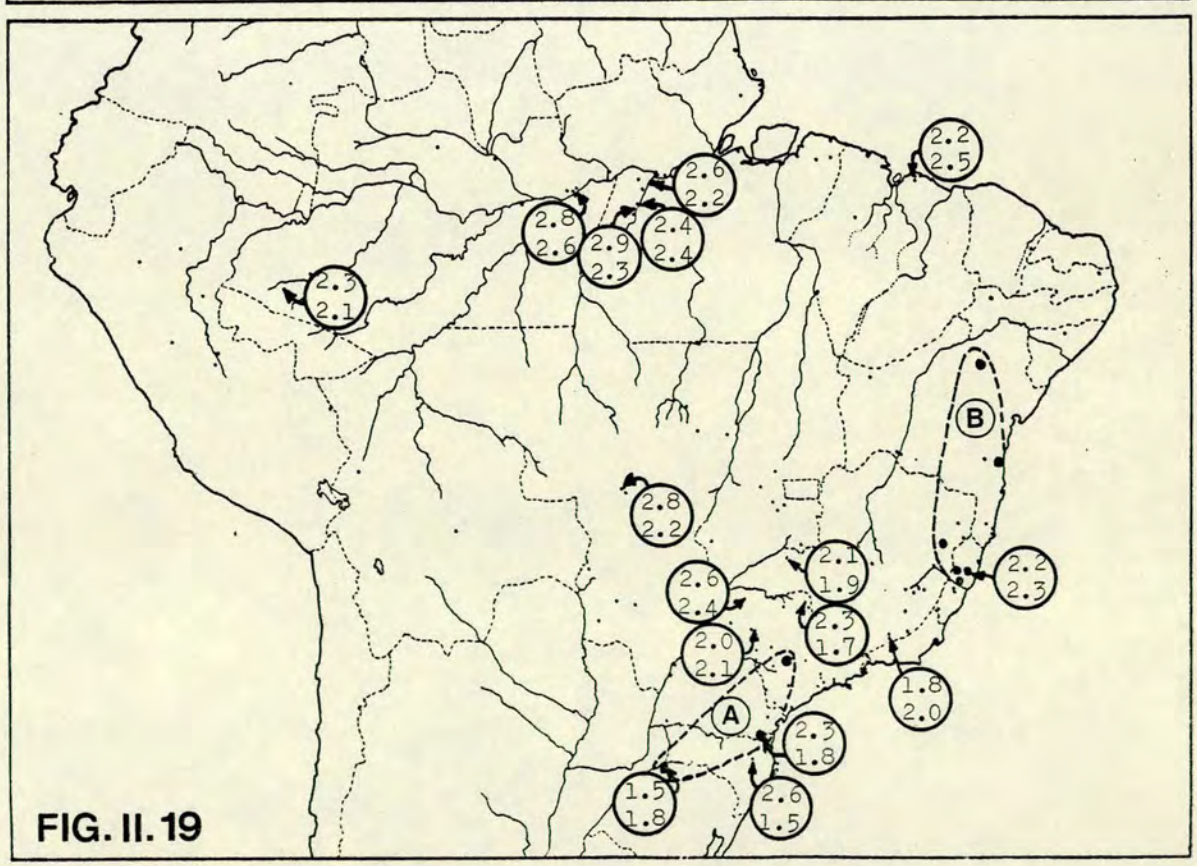


FIG. II.19

Fig.II.20 - Conspicuousness of the sagittal crest in skulls of adult males.

Circles - samples in which crests were noted to be "poorly developed"

Black dots - samples in which crests were noted to be "particularly prominent"

Triangles - samples where crests were noted to be "evident"

The diagonal gives a coarse eastern limit for the area of "poorly developed" crests. The curve in southeastern Brazil delimits the area of the "prominent" crests.

Half covered circles indicate localities where crests seemed to start their development at a relatively greater age, so that only old animals would show the full crest development.

Fig.II.21 - Colour of ventral hairs

Black dots - ventral hair is generally dark brown

Triangles - ventral hair is generally red

Squares - ventral hair is generally dark brown tinged with red.

Circles - ventral hair may be either light brown, orangish light brown, reddish light brown or yellowish light brown. The only common feature is that all samples include at least one animal with yellowish ventral hairs.

Crosses - samples that do not fit any of the above categories (although they may partially overlap with them, e.g. a sample where all animals have reddish light brown ventral hairs).

The lines shown are the isophenes for the various categories.

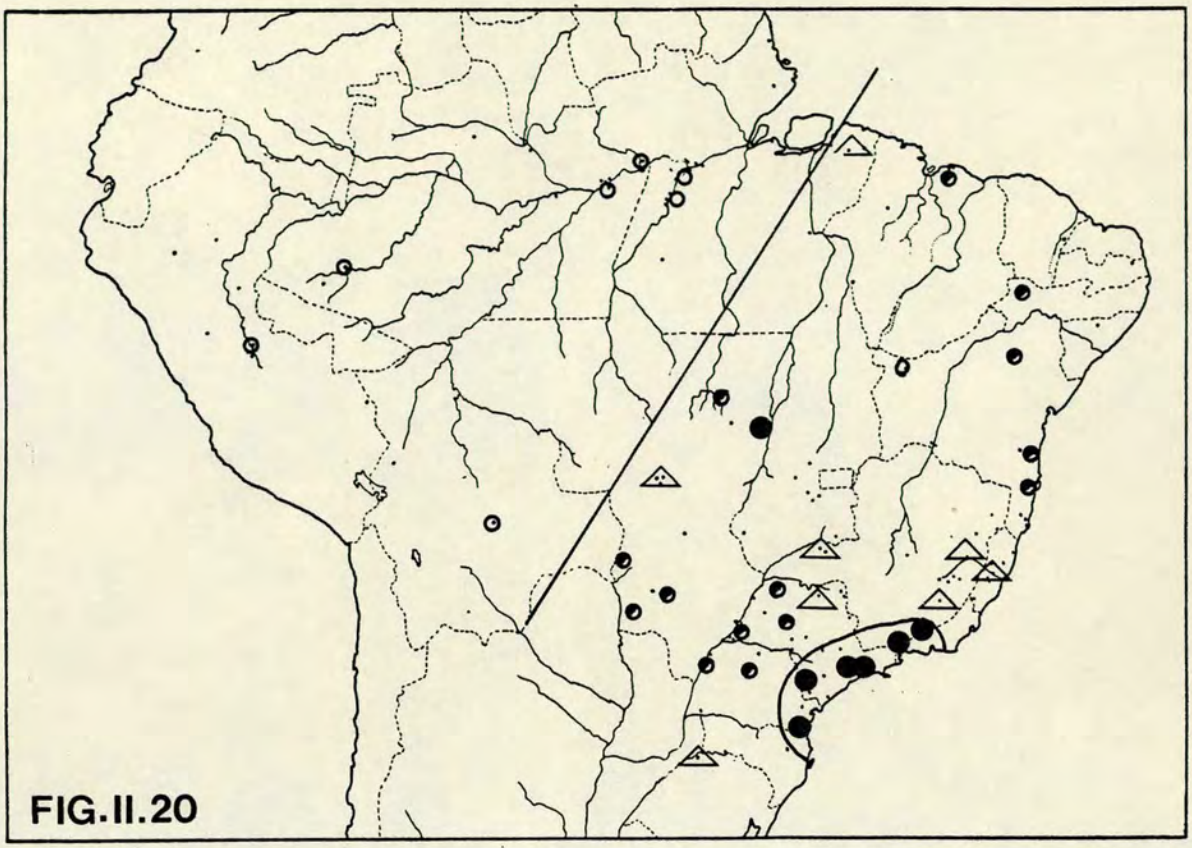


FIG.II.20

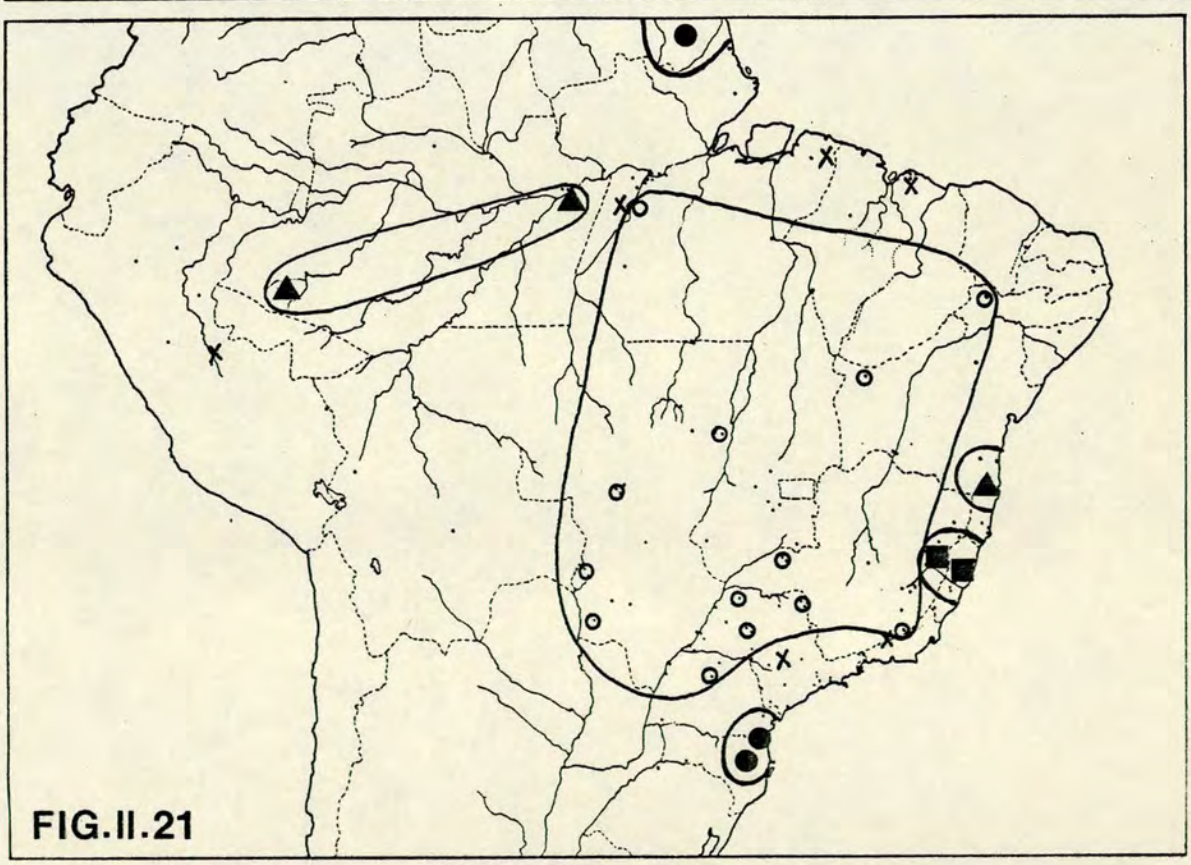


FIG.II.21

Fig.II.22 - Cap colour

Black dots - locality whose sample includes some animals with brown caps.

Circles - localities where the animals have either dark brown, blackish brown or black, but not brown, caps. (As the category "brown" is the least likely to be confounded with others, it is the only one for which an isophene is drawn and used in the analysis.)

Fig.II.23 - Dorsal stripe (presence and distinctiveness)

Dots - localities where the animals generally have dark dorsal stripes, usually quite nitid, but not necessarily so.

Circles - localities where the animals' backs may be slightly darker than their flanks (i.e. a diffuse dorsal stripe may be recognized).

Triangles - localities where the animals have backs concolorous with flanks.

A straight line indicates the eastern limit of the area where animals have nitid dorsal stripes. An isophene is drawn for the area of diffuse dorsal stripes. The areas with concolorous flanks and back are evident without isophenes.

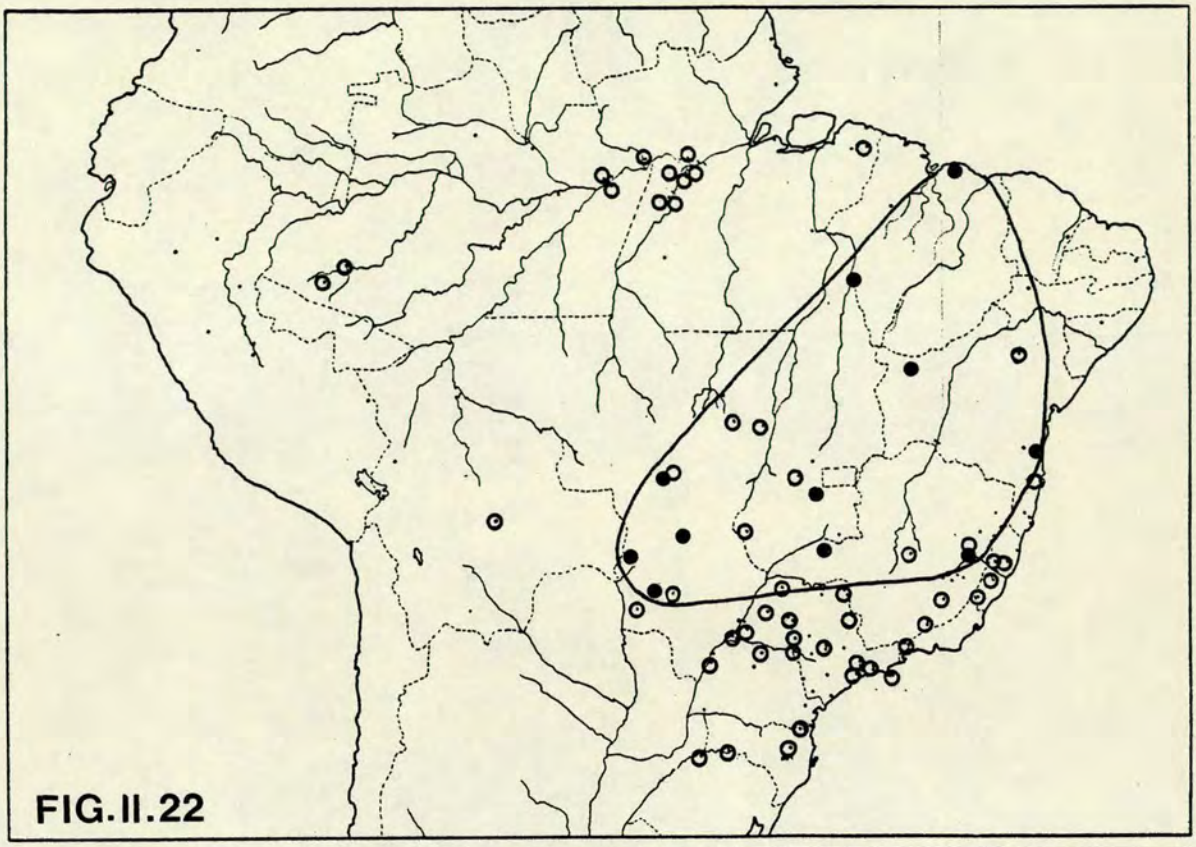


FIG. II.22

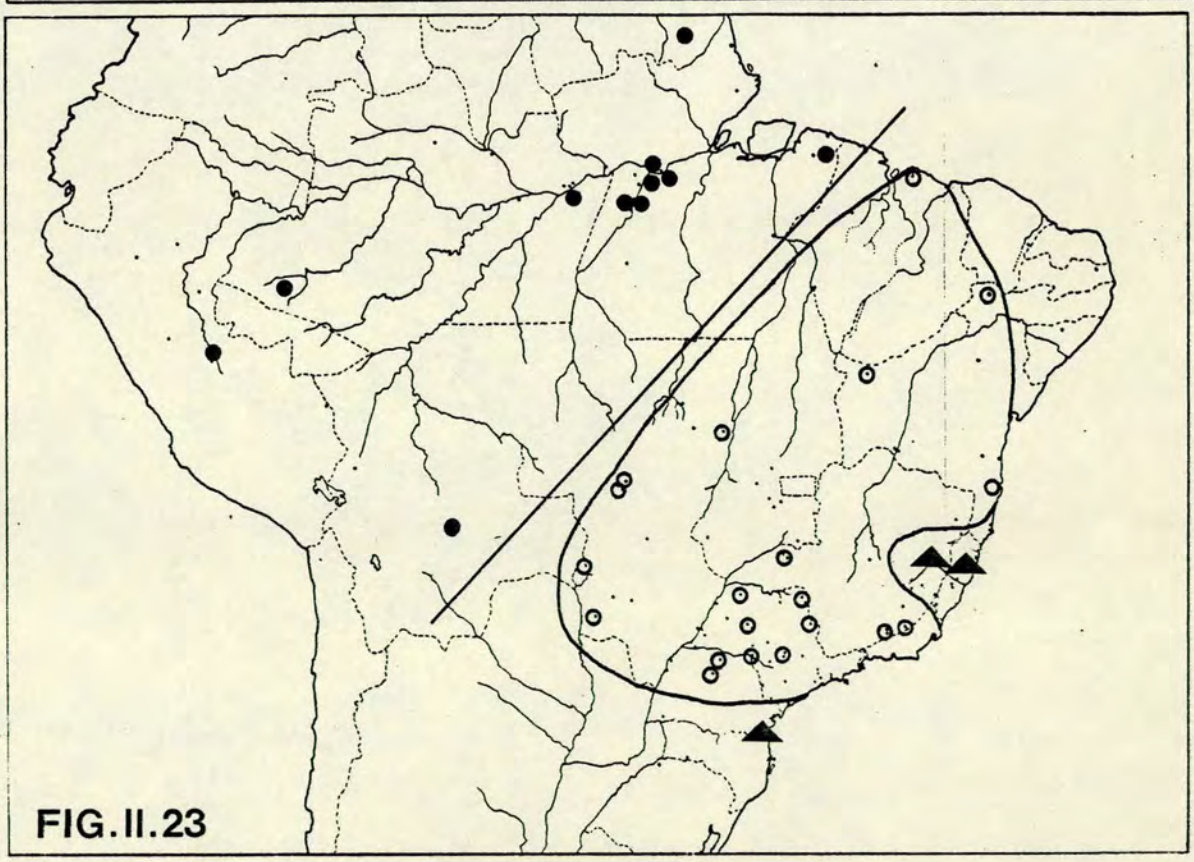


FIG. II.23

Fig.II.24 - Colour of the flanks hairs.

Black dots - animals with reddish brown flanks (shoulders occasionally lighter)

Empty squares - flanks are of various shades of brown; shoulders generally lighter in colour (e.g. yellowish).

Black triangles - most animals have either blackish brown or black coats.

Black squares - Flanks colours include black, light brown, reddish brown and yellow forming a rather fixed coat pattern.

Crosses and circles - flanks may be any shade from yellowish light brown to dark brown, the common feature being that in many samples (circles) flanks are frequently greyish brown.

For the first four categories, solid-line isophenes are drawn.

In some samples, adult females occasionally had a few white hairs on the nape and anterior back. A dotted isophene indicates the area concerned (the localities are listed in the section on sexual dimorphism).

Fig.II.25 - A and B
A) Variability and heterogeneity in flank colour.
Black dots - some animals had flanks with a mottled appearance.
Circles - flank colour seemed particularly variable between individuals.
Isophenes from Fig. II.24

B) Type localities
The arrows indicate the type localities of most of the described forms for which the type locality is known. In some cases only a number is used (without arrows) indicating that the precise type locality is not known, only the general area. See text (RESULTS) for the list of forms.

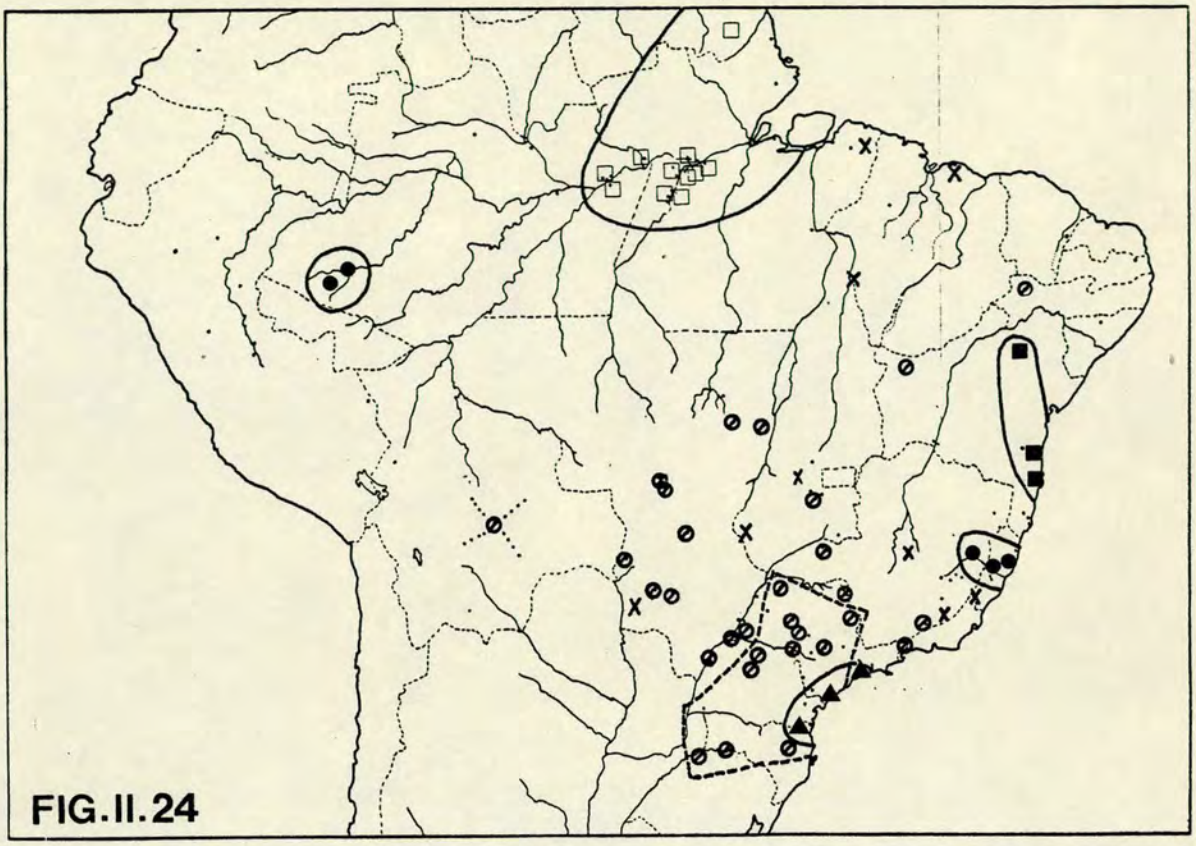


FIG.II.24

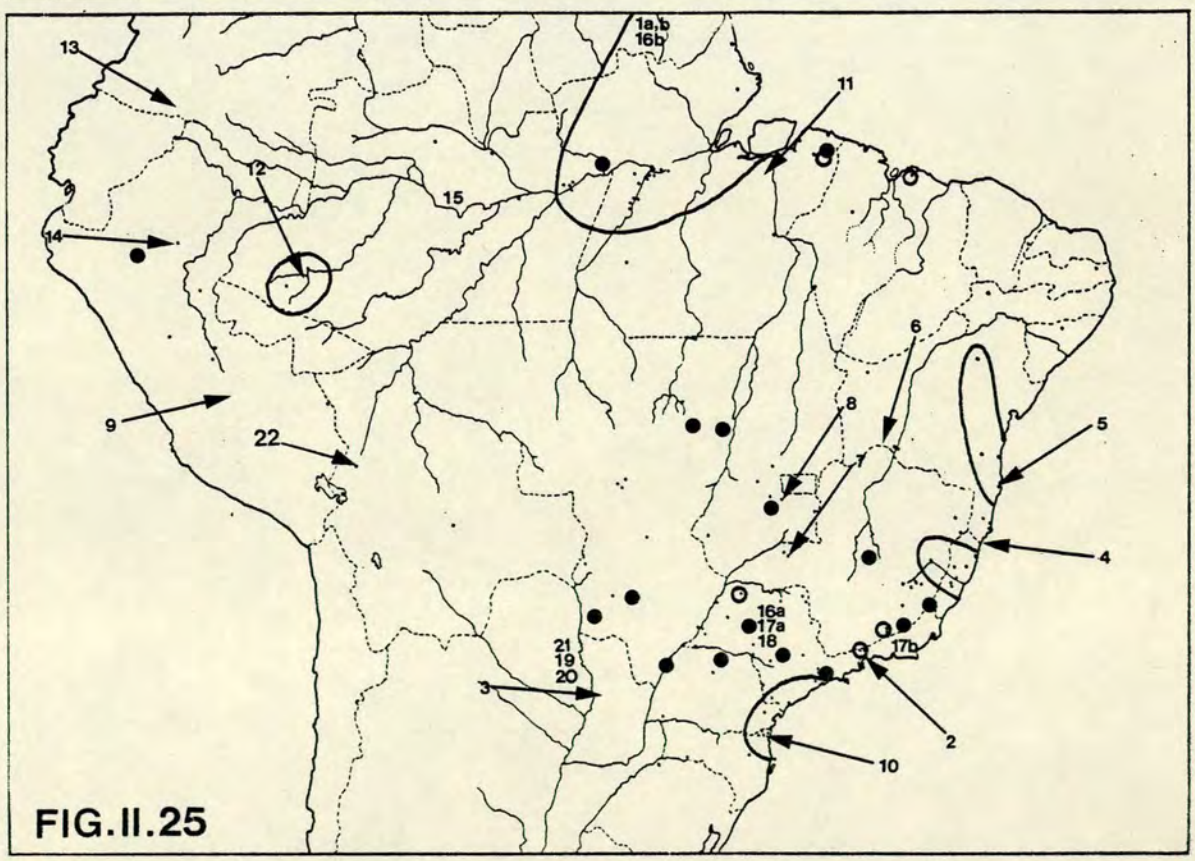


FIG.II.25

Fig.II.26 - Cap shape.

Large dots are localities whose samples had at least 4 adult skins. Small dots, as in the other figures, are localities with smaller samples. The smaller samples were used to determine the fine limits of the isophenes, but no isophene is based only on the smaller samples.

Area A - animals from this area seem not to develop long tufts of hairs even as adults. The forehead pattern varies considerably. (Some possible shapes are illustrated.)

Area B - in this area the adult animals may or not develop tufts. The proportion of tufted adults varies considerably. Females seem more prone to develop long tufts than males. There are often dark hairs on the forehead (a patch above each eye). The anterior part of the cap generally forms a nitid "V" on the forehead.

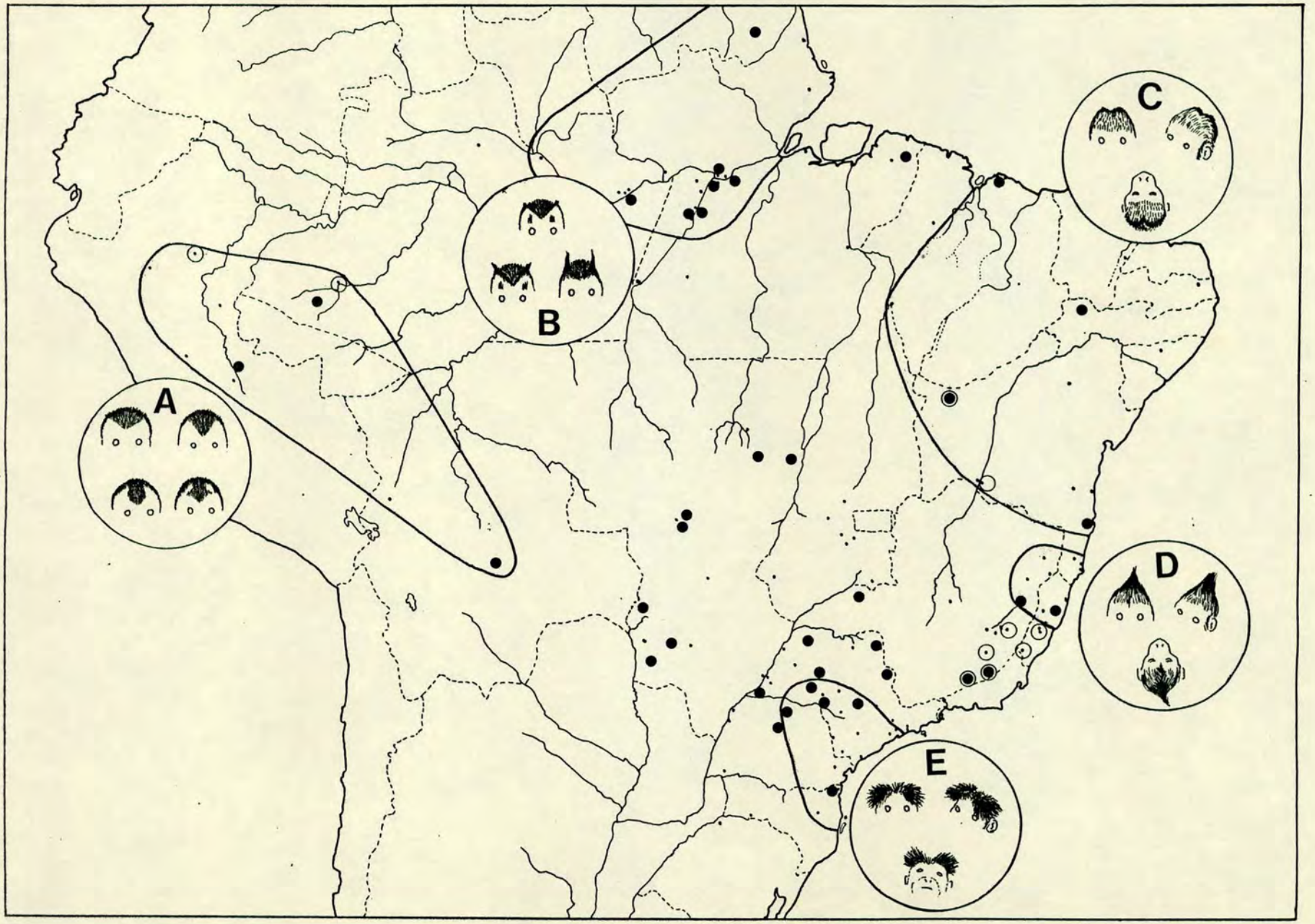
Area C - most adult animals in this area develop two tufts of longer hairs on the cap, but these hairs are bent backwards. A wide band of lighter colour separates the cap from the face. Seen from the front, the animal may look tuftless. The crown is not necessarily homogeneously dark. This category includes several sub types which might, with a larger sample, reveal a more detailed pattern.

Area D - in this area most adults develop two tufts, but these converge on the top of the head, giving the impression that there is only one. See also Fig.II.5 (bottom).

Area E - in this area most adults have two hair tufts. Their aspect is fairly variable, and the only common feature to samples from this area is that a few animals (generally females) have their tufts torsioned forwards and sideways. The most common type of tuft is, however, like that pictured in Fig.II.5 (top).

Outside of these five areas the animals' caps do not seem to have any distinctive feature. Tufts may be formed or not; if formed they are generally erect and well separated, and what seem to be intermediates between those of areas D and E may be observed; the forehead pattern may be similar to those of areas A,B or C.

Open circles indicate samples where some animals seemed to be intermediates between forms of neighbouring areas.


A
B
C
D
E

Cap shape has been used as a taxonomic character by most researchers who studied Cebus, but the character does have its limitations. Firstly, the full development of the tufts is only attained in adult animals; the cap shape in immature animals is more or less similar in all localities and is reminiscent of that of untufted species. Secondly, the cap shape may be variable within localities. Thus, even if geographical patterns can be discerned, not all specimens of a given area necessarily look the same. Cap shape is a useful character, but the identification of most forms requires the joint use of several characters.

Integration of characters (both qualitative and quantitative)

Considered separately, each character conveys only limited information about geographical patterns, but all seem to indicate a relatively indistinct population in the central part of South America, with more distinct populations around it, namely in western Amazonia, in the Guyanas region, and in various points along the Atlantic coast. Results from qualitative and quantitative characters seemed not to be contradictory, so the information from all characters was pooled together in an attempt to highlight and perfect the geographical pattern.

Although the isophenes in Figs.II.18 to II.26 are certainly not identical, when they are put together (Fig.II.27) one can see that they tend to concentrate in some areas. The accumulated isophenes loosely delimit a number of regions where a number of characters have distinctive features. Within each of these general

Fig. II.27 - Accumulated isophenes/limits of distribution (qualitative characters only)

——— - from Fig.II.19 (vomer shape)

xxxxxxxxxx - from Fig.II.20 (sagittal crest)

------- - from Fig.II.21 (colour of ventral hairs)

-∴-∴-∴ - from Fig.II.22 (cap colour)

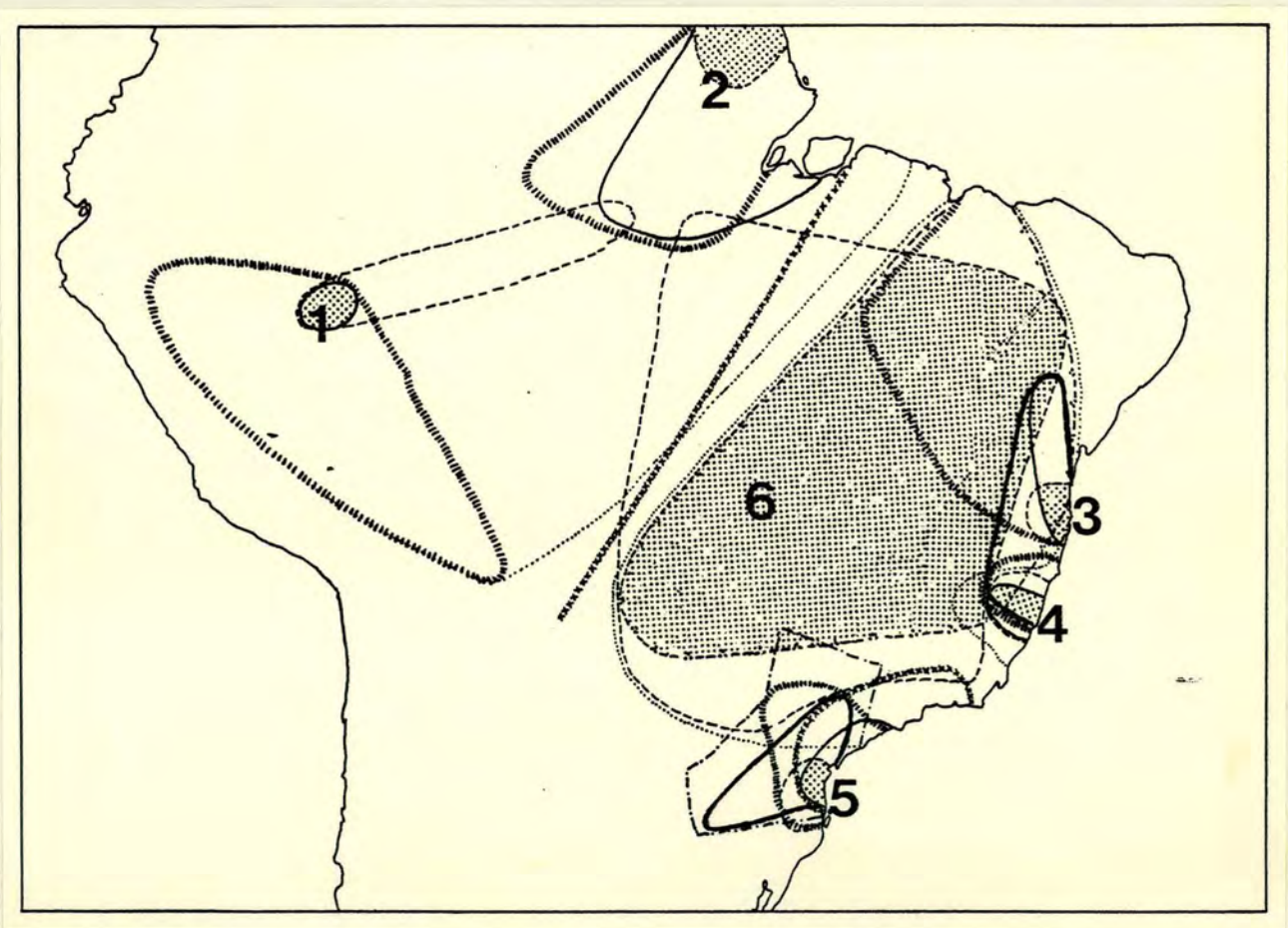
..... - from Fig.II.23 (dorsal stripe)

——— - from Fig.II.24 (flank colour)

-·-·-·-· - from Fig.II.24 (occasional white hairs on flanks)

mmmmmmmmmm - from Fig.II.26 (cap shape)

The accumulated isophenes identified several regions, within which are indicated by shading the areas of maximal overlap. The numbered areas are discussed in the text.



regions, a zone of maximum overlap (a "core area" sensu Vanzolini and Williams 1970) can be identified. Fig. II.27 shows the six regions that can be recognized on the basis of the qualitative characters. To each corresponds a core area (shading), although the number of characters characterizing a core area is not necessarily the same in all cases. This figure must also be compared with the summary figures for quantitative characters (Figs.II.13 and II.17). The regions and their core areas are:

1. Western Amazonia (with core area in the high R.Juruá)

Flank colour and skull size distinguish the animals from the banks of R.Juruá. Unfortunately the nearest neighbouring samples are very far from R.Juruá, so it is not possible to estimate how large this area really is. The colour of ventral hairs suggests that the populations from this area are not different from those of R.Tapajós; the cap shape does not distinguish the Juruá populations from those of Peru and Bolivia. However, colour of ventral hairs is a problematical character in the present study, and the category of cap shape for this area is quite broad. The multivariate analysis on skull characters indicates that animals from AM1 constitute a very distinct group; it also suggests (males data) some similarity between the populations of the high Juruá and the Bolivian sample. One would expect animals from the core area to have:

- poorly developed sagittal crests
- relatively large skulls
- reddish or red ventral hairs in most specimens
- dorsal stripe generally nitid and darker than flanks
- flanks generally reddish brown, with shoulders of similar shade

- dark cap (i.e. not brown) without tufts

2. Middle to low Amazon, and Guyana(s) , with core area in the French Guyana

Cap shape, colour of ventral hairs and flank colour distinguish the animals from this area. On the basis of uni and multivariate analysis, the population of the middle/low Amazonas are more similar to those of northeastern Brazil than they are to those of R.Juruá, although several of the remaining characters seem to associate all Amazonian animals and distinguish them from those of the northeast. As I have no adequate skull sample from this core area, its similarity with the others cannot be assessed. One would expect animals from the core area to have:

- poorly developed sagittal crests
- dark ventral hairs
- a dorsal stripe darker than flanks
- flanks of various shades of brown, with shoulders generally lighter in colour
- some dark hairs above each eye (not all specimens)
- dark cap (i.e. not brown) forming a "V" on the forehead; tufts may be formed along that "V", and females seem to be more prone to develop tufts than males.

3. Eastern Bahia, with core area around BA3 and BA5

Colour of ventral hairs and colour of flanks identify the animals that come from this region. Since I have no adequate skull sample from the core area, its similarity with the others cannot be assessed. Cap shape and cap colour indicate homogeneity for the

whole northeastern of Brazil, but in Fig.II.13 there is no indication of affinity between this area and the northeast. It should be noted that the cap shape category used for this area includes several sub-types, so the area is not so homogeneous as it looks from the corresponding map. One would expect animals from the core area to have:

- red or reddish ventral hairs
- sagittal crests apparently with delayed development
- flanks with a fixed colour pattern including black,yellow and light brown
- cap frequently light coloured (brown); although tufts develop, they are generally bent backwards.
- a stripe of light coloured hairs (or a mixture of light and dark hairs) between eyes and cap.

4. Eastern Minas Gerais, and Espírito Santo north of R.Doce, with core area along the northern bank of R.Doce

Animals from this rather restricted area are distinguished by the following characters: colour of ventral hairs, [absence of] dorsal stripe, flank colour, and cap shape. Skull univariate analysis suggest that animals from this area have some affinity with those of western Bahia, western Minas Gerais and SE Goiás. Although the multivariate analysis does not contradict such similarity, it indicates that animals from eastern Amazonia (males data) are equally similar. Vomer shape provides a further indication of affinity between this area and area 3. One would expect animals from the core area to have:

- reddish brown ventral hairs

- sagittal crest generally well developed
- dark cap (not brown)
- absence of a darker dorsal stripe
- reddish brown flanks
- convergent tufts giving the impression that there is only one

5. Coastal areas of São Paulo, Paraná and Santa Catarina, with core area around SC1+2+3+4

Animals from this area are distinguished by the following characters: sagittal crest, flank colour, colour of ventral hairs, dorsal stripe, and cap shape. Skull univariate analysis suggests high affinity between the samples of coastal Santa Catarina and the multivariate analysis suggests that these constitute a quite distinct group. Animals from the core area should have:

- very conspicuous sagittal crests
- dark ventral hairs
- dark cap colour (not brown)
- black or blackish brown flanks
- two well developed hair tufts on the cap. These may be erect or torsioned sideways and forwards.
- in adult females white hairs may be found on the anterior part of back and flanks, mixed with the dark ones
- relatively large skulls.

6. a very large area which includes central and northeastern Brazil (states of Goiás, SE and E of Mato Grosso, Maranhão, W of Pernambuco, W of Bahia, NW of São Paulo and Paraná, W of Minas

Gerais). The core area is slightly smaller, and located in the centre of this vast region, but is still quite large.

The characters which indicate this area as a unit are: colour of ventral hairs, flank colour, cap colour and dorsal stripe. The isophenes of these characters tend, however, to cross previously defined areas, particularly with area 3. Univariate skull analysis indicates that there is some affinity between all samples of this vast area, where skulls are relatively small. In the multivariate analysis, almost all localities of this area tend to be lumped together in an indistinct cluster; the exceptions are samples from MT, which seem to be less similar to the other samples of this region. If a core area can be recognized for this region (see discussion), its animals should have:

- (occasionally) yellowish brown ventral hairs
- (occasionally) greyish brown flanks
- (occasionally) brown caps
- (not always) diffuse dorsal stripes.
- relatively small skulls

Re-assessment of the described forms of tufted Cebus

Do the forms described to date fit the expected phenotype for the areas where their type locality is?

A list of the type-localities included in Fig.II.25 follows. For some forms the precise location is not indicated in the map. In these cases there are no arrows: the number is placed roughly near the region where the type should have come from. This figure does not include all described forms (more than 45 have been described),

but only the ones for which a type-locality has been specified. I also excluded the type locality of the form margaritae (Isle Margarita, Venezuela) since it is not covered by my sample.

1a. apella Linnaeus 1758 - according to Hill 1960 (p.463) the type locality has been restricted to the Guyanas. Linneaus mentioned only "America". No type has been preserved.

1b. trepidus Linnaeus 1766 - this form should inhabit Surinam, according to Edwards (1758), on whose work Linnaeus based his description. No type has been preserved.

2. nigritus Goldfuss 1809 - according to Hill 1960 (p.486) the type locality of this form is Rio de Janeiro, Serra dos Órgãos. I was not able to check this information with the original description. No type seems to have been preserved.

3. cay Illiger 1804/1811 - according to Hill 1960 (p.477) the type locality of this form is Paraguay, left bank of R.Paraguay. This information is not mentioned in Illiger's paper, but in Azara's account (on which the description is based). No types seem to have been preserved.

4. robustus Kuhl 1820 - Although Kuhl did not clearly name the locality, the animals on which the form is described came from Morro d'Arara (see Wied-Neuwied 1820, p.227). According to Pires (1965), Vieira (1955) was the first to restrict the type-locality to Morro d'Arara [R.Mucuri, State of Bahia, Brazil]. The types seem to have been lost (see Pires 1965, p. 10).

5. xanthosternos Kuhl 1820 - Although Kuhl did not name it, the animals on which this form is described came from Boca d'Obu, Rio Belmonte [State of Bahia, Brazil] (see Wied-Neuwied 1820, p.327). Type (not examined) in Leyden (a lectotype, according to Pires 1965,p.11; a syntype, acc.to letter from the Museum curator).

6. libidinosus Spix 1823 - the type-locality is R.Carinainha (=Carinhanha), a *tributary* of R.S.Francisco [state of Bahia, Brazil], according to the original description. Type in Munich (according to Hill 1960, p.480), not examined. A colour picture of this form is given by Spix 1823. Types (cotypes acc. to Lima 1945,p.144) in Munich , not examined.

7. versuta Elliot 1910 - according to the original description, the type locality of this form is R.Jordão, western part of [the State of] Minas Gerais, Brazil. Type in London, examined.

8. elegans Geoffroy 1850 - although the original description does not mention it, it is written on the base of the mounted type that the animal came from the woods near the Rio los(=dos?) piloes(=Pilões), Province(=State) of Goyas(=Goiás), Brazil. The same information is given by Hill 1960 (p.477). Type in Paris,

examined.

9. peruanus Thomas 1901 - the original description mentions Marcapata, Huanapata, Inambari Valley, SE Peru, as the type-locality. This locality cannot be precisely pinpointed (P.Vanzolini, pers.comm. based on Vaurie 1972). Type in London, examined.

10. caliginosus Elliot 1910 - according to the original description, the type locality is "Sta.Catharina, São Paulo, Brazil". Napier (1976) indicates Colonia Hansa [State of Santa Catarina] as being the type-locality. The latter is probably correct, for the specimen was originally at the São Paulo Museum, where there are several specimens from Colonia Hansa collected at the same date and by the same collector as the type. Type in London, examined.

11. tocantinus Lonnberg 1939 - type locality is Cametá, R.Tocantins, according to the original description. Type in Stockholm, not examined.

12. juruanus Lonnberg 1939 - the original description indicates that this form inhabits various localities along the R.Juruá (Igarapé do Gordão, Igarapé Grande, Lago Grande) and along the R.Eiru (Santo Antonio). Type in Stockholm, not examined.

13. magnus Pusch 1941 - according to the original description, this form comes from R.Putumayo, Colombia (1 N, 76 W). Type (a male according to Hill 1960,p.471) confirmed to be in the Museum fur Naturkunde, E.Berlin, not examined.

14. maranonis Pusch 1941 - according to the original description, this form comes from Hamburgo, Peru (5 S, 75 W). Type (a male according to Hill 1960,p.474) confirmed to be in the Museum fur Naturkunde, E.Berlin, not examined.

15. macrocephalus Spix 1823 - according to the original description, the type locality is Lago Catuá, near R.Solimões [State of Amazonas, Brazil]. Fig.II.25 does not indicate the exact location of this lake. Type confirmed to be in Munich, but not examined. A colour picture of this form is given in Spix 1823.

16a and 16b. cucculatus Spix 1823 - according to the original description the type locality is "sylvis provinciae St.Pauli et Guyanae". These regions are very far apart. It is likely that the ascribing of the same form to both is a mistake. Holotype reported to be in Munich (Hill 1960, p.483), but presently considered lost (pers. comm. from the curator). Spix (1823) provided a colour picture of this form.

17a and 17b. xanthocephalus Spix 1823 - according to the original description, the type locality is "sylvis provinciarum R.Janeiro et St.Pauli", but the form described and pictured by Spix is unlikely to have come from either Rio de Janeiro [State] or S.Paulo [State] - my sample indicates that this form is not found south of the State of Bahia. Type confirmed to be in Munich, but not examined. A colour picture of the form is given by Spix 1823.

18. vellerosus Geoffroy 1851 - according to the original description, this form comes from the province (=State) of São Paulo. Types in Paris, examined.

19. morrulus Pusch 1941 - according to the original description, type locality is Santa Barbara, Central Paraguay. Type (a female according to Hill 1960,p.477) confirmed to be in the Museum fur Naturkunde, E.Berlin, not examined.

20. chacoensis Pusch 1941 - according to the original description, type locality is the Chaco Paraguayo. Type confirmed to be in the Museum fur Naturkunde, E.Berlin, not examined.

21. azarae Rengger 1830 - Rengger names the form found by Azara (1809) in Paraguay. No particular type locality seems to have been indicated, and no types seem to have been kept.

22. sagitta Pusch 1941 - type locality is Chimati, Bolivia; type in London, examined.

Table II.9 summarizes the results of the comparison of the original description for the various forms of tufted Cebus with the phenotype I expect for the areas where the types are said to come from.

The following forms cannot be included in Table II.9 because their type localities have not been indicated by their authors:

Brisson's (1766) fuscus, niger, cornutus, flavus, variegatus [no types]
Linnaeus' (1766) fatuellus, based on Brisson's cornutus [no types]
Kerr's (1792) fulvus [no types]
Buffon's (1767) various forms, described but not named [no types]
Audebert's (1797) various forms, described but not named [no types]
Geoffroy's (1812) cirrifer [type in Paris, examined]; , variegatus [type in Paris, examined] and niger (based on one of Buffon's unamed forms) [no type]
Kuhl's (1820) frontatus [type in Paris, examined] and lunatus [holotype in Leyden,not examined]
Cuvier's (1820) monachus [no type]
Cuvier's (1819 and 1819) various forms, described but not named [no types]
Pucheran's (1857) crassiceps [type in Paris,examined] and hypomelas [type in Paris,examined]
Gray's (1865) leucogenys [type in London, examined] and pallidus (based on Geoffroy's elegans) [type of elegans in Paris, examined]

TABLE II.9
COMPARISON OF LITERATURE DESCRIPTIONS AND OBSERVED SAMPLES

Described forms:	The described form: Does not disagree with the phenotype observed in the area where the type locality is. A "*" is used if the described form is just one of the possible local phenotypes	The described form: Does not agree with the phenotype observed in the area where the type locality is
	(brackets are used in the cases in which my sample for the area near the type locality did not allow firm conclusions)	
APELLA	*X	
TREPIDUS	*X (on the basis of Edward's 1758 plate	
NIGRITUS	*X (fide description of nigritus in Hill 1960)	
CAY	(X)(on the basis of the description by Azara 1809)	
ROBUSTUS	X	
XANTHOSTERNOS	X	
LIBIDINOSUS	(*X)	
VERSUTA	*X	
ELEGANS	*X	
PERUANUS	(X)	
CALIGINOSUS	*X	
TOCANTINUS		(X)
JURUANUS	X	
MAGNUS	(*X)	
MARANONIS	(X)	
MACROCEPHALUS	(*X)	
CUCCULATUS		X
XANTHOCEPHALUS		X
VELLEROSUS	*X	
MORRULUS	(*X)	
CHACOENSIS	(*X)	
AZARAE	(*X)	
SAGITTA	(X)	

Note: only the characters mentioned in the original description can be checked; the relevant ones may have not been included in the description.

Pusch's (1941) avus [based on two live animals. One type skull confirmed to be in the Museum fur Naturkunde, E.Berlin, not examined.] Pusch's types should be found.

I was not able to examine the original descriptions of nigritus Goldfuss 1809, cristatus Cuvier 1820 or paraguayanus Fischer 1829, therefore I do not know whether a type locality has been indicated for these forms. According to Hill (1960) nigritus Goldfuss 1809 is based on Buffon's (1767) figure of "sajou negre", for which Buffon indicated no type locality. Hill (1960) stated that Serra dos Órgãos is the type locality, but this needs checking.

Table II.9 shows that most types do not disagree with the phenotype expected from the area where the type locality is. However, this does not mean that the described types represent the population of a given area, because in several cases more than one phenotype can be found in the population around the type locality. For example, the form elegans Geoffroy 1850 (from locality GO-14, or 8 in Fig.II.25B) was described as having fur "beau fauve doré au fauve grisâtre....barbe d'un roux doré, et de long poils noir sur la tête, forment une sorte de toupet, divisé en deux parties par une goutière médiane". Animals from localities within 100 km of the type locality may or not correspond to the description of elegans; adult animals from GO-6 may have a divided tuft but have heterogeneous greyish brown fur, whereas adult animals from GO-3 may have fur similar to the type of elegans, (yellowish light brown with some red) but not long tufts. The description of elegans may have pictured the type specimen well, but it did not allow for the variation within the population.

Another example is the form versuta Elliot 1910; the original

description indicates that this form is distinguishable from closely related forms by the cap shape, in particular by the breadth of the tuft ridges; the fur was described as Prout brown with bistre flanks (Elliot did not describe the variation in the dorsal stripe colour existent in his sample). My sample from MG-14, less than 50 km from the type locality MG-13, includes animals similar to those described, but also animals with upright tufts and yellowish light brown fur (although these phenotypes are unusual for that area).

The main point is that, if the characters indicated in most descriptions were to be accepted as race-specific, one would have to recognize two or three races in most localities. For such a variable species, the description of individuals rather than populations cannot lead to any meaningful arrangement.

DISCUSSION

> "Systematic research, when not conducted with a theoretical approach, inevitably leads to the construction of artificial systems, for the emphasis will be on species identification, and not on the evolutionary process. It is vain and frustrating to try interpreting revisions not originally written to be interpreted; alpha-systematics is not the basis for beta-systematics."
>
> (translated from Vanzolini 1970)

THE NOMENCLATORIAL ASPECT OF *CEBUS APELLA* SYSTEMATICS

Most taxonomic work on *Cebus* has been done with little concern for natural units; any specimen that differed from previously described forms was given a new name and species status, without intra-population variability being investigated. Although this approach had to be used by the early taxonomists due to scarcity of specimens, it lasted for longer than the amount of material justified. *Cebus* taxonomy has been further complicated by:

- the acceptance, as recognizable taxa, of insufficiently characterized forms (e.g. forms for which there is no type and whose type locality is unknown; forms based on abnormal captive specimens; forms whose descriptions do not match the accompanying figure, etc..)
- uncritical revisions which were either a simple compilation or where interpretation was done and synonymies were established without careful re-examination of the original informaton.

These procedures, plus the imprecision of the early diagnoses, resulted in a vast number of forms being accepted, which did not

necessarily correspond to natural groups, and whose naming is, in many cases, questionable. One example will illustrate how the confusion builds up:

The form frontatus was (briefly) described as a species (Kuhl 1820), based on animals kept in captivity and of unknown origin. The holotype (and [although the type locality is unknown!] a "paratopotype" (Rode,1938)) are housed at the Paris Museum. Both types show what seems to be aberrant (asymmetric) whorls in the cap. This aspect was not mentioned by Kuhl in his description, and does not show in the picture he chose to represent the form (Audebert's (1797) figure of "Sajou var.A").

Pinto (1941) and Vieira (1944) identified some specimens at the Sao Paulo Museum as C.frontatus, using as a distinguishing feature the "particular disposition of the head's hair, which formed a kind of a depressed cap projected sideways over the forehead". Pinto (1941) provided a drawing of this form and Vieira (1944), on the basis of 5 animals in S.Paulo museum, gave its geographic distribution. Both authors considered this form to be a species.

Hill (1960) accepted Pinto's and Vieira's identification of frontatus, but, instead of illustrating the form with Pinto's (1941) drawing of the identified specimens, he provided his own drawing of frontatus. His drawing was based on a sketch of the holotype made by P.Dandelot, but the final drawing is quite different from the type. Thus, even if Hill, Vieira and Pinto had in mind a particular form with a known geographical distribution, that form is not what Kuhl had named frontatus. Also, Hill considered frontatus to be a race, "presumably" allopatric with other races.

The first mistake seems to be Pinto's (1941) identification of the specimens as frontatus. I do not see in Kuhl's description any statement that justifies Vieira's recognition of a "sideways projecting" cap. This form is better considered unidentifiable, since its description is poor, the drawing in Audebert (1797) is inconclusive as far as cap is concerned, and the types seem to be aberrant specimens of unknown origin. More seriously, the reduction of frontatus to race status by Hill produced an internal inconsistency. Vieira (1944) implied that his frontatus coexisted with other forms (for him, other species), a detail that Hill(1960) skipped, when he "presumed" that the forms were allopatric. To be consistent with the information in the literature, Hill should either have considered frontatus as a good species (therefore isolated from other sympatric forms), or else as an individual variation, but not as a race.

Difficulties like the above abound in Cebus taxonomy, so that tidying up the inconsistencies, identifying the recognizable forms and naming them becomes a long and intricate task. The revision of the subject involves not only the synonymising of forms and the finding of their "correct" name (i.e., according to the current code of nomenclature). To characterize biologically sound races, redescriptions are required in several cases, to incorporate the range of variation of each race, or to complement insufficient original descriptions.

A full revision will not be presented here for two reasons:
a) I have not examined all the types; also, in some cases the information I have from the region of the type locality is

insufficient to decide whether the type specimen is really different from the forms seen elsewhere.

b) To define races it is important to understand the relationship between the populations of the various areas, so that a race is not recognized in hybrids. Although my study allowed a preliminary picture for some areas, there remain several critical points to be clarified (particularly the affinities of the populations of central Brazil).

I do not want to name forms before I am sure of their relationship, but I will examine the obtained evidence from an evolutionary point of view, to provide the basis for a tentative arrangement.

THE BIOLOGICAL ASPECT OF CEBUS APELLA SYSTEMATICS

Subspecies resemble species in that each is separated from the others by some degree of character discontinuity. Character discontinuity implies differentiation between populations. Although such differentiation may be produced by a number of evolutionary mechanisms, one generally looks for evidence for geographical isolation first. I shall initially assume that differentiation within the species occurred in geographically isolated populations, and then examine alternative explanations.

The expected pattern for a multi-race species

(assuming race differentiation with geographic isolation)

If there has been geographical isolation, the discontinuities between the differentiated populations should be reflected in the

geographical distribution of the various morphs.

For a given character, the pattern of morphs distribution could be: stability throughout the area; irregular variation throughout the area; gradual variation in a particular direction; stability in some areas, bordered by areas of either abrupt or gradual transition. Although each character will have its own morph distribution, if there had been geographical isolation in the past, the various characters should indicate coherent patterns. For instance, various characters may consistently indicate the same geographical region as being an area of character stability (i.e., an area where several characters are less variable). Such regions have been called "core areas" by Vanzolini & Williams (1970), and I will retain their terminology. Provided that the stability in the core area is not an environmental product, it may be seen as an indication that these populations are sharing more genes than they share with populations of other areas. This could be interpreted as being due to previous isolation of the "stable" populations.

Sub-specific divergence is potentially reversible, so in the absence of the barrier that had presumably isolated the core area populations, all forms may tend to merge into a new unity.

Panmixy over large areas may be unlikely, but some mixture is to be expected; the extent to which it is observed will depend on various factors: the time since the disappearance of the barrier, the velocity of dispersal of the previously isolated populations, the differential fitness of the various hybrids, etc.. If the regions separating core areas are seen as areas of secondary contact between previously isolated populations, we might expect for these regions:

a) characters to have an intermediate aspect between those of the

adjacent core areas (there might be a gradient between the extremes),

b) the coexistence of the morphs typical of the adjacent core areas

It should however be noted that animals in the zone of secondary contact do not have to be obvious intermediates between the forms of the core areas, because the characters are not necessarily controlled by simple genetic systems. Also, if the population in the areas of secondary contact received genetic contribution from more than one core area , it would be even more difficult to recognize a blend.

The evidence compared with the expected pattern

The morphological data yielded a geographical pattern in which six areas were recognized. In areas 1 to 5, despite large individual variation in all characters, it was possible to distinguish a set of features exclusive to each area. The populations of each of these 5 areas seem to be differentiated and can be said to have undergone a certain amount of speciation.

Area 6 cannot be interpreted as the first five. Animals from this vast area may share some common features (occasional yellowish brown coat, occasional diffuse dorsal stripe, occasional greyish brown coat, occasional yellowish brown ventral hairs). However, only the last morph seems to be exclusive of this area, and this character is problematical. Characters cap shape and flank colour, generally useful in characterizing animals from the other 5 areas, do not have exclusive morphs in area 6. As far as I can detect, the animals of this area do not have the typical features of areas 1 to 5, but do not have exclusive morphs of their own. None of the examined

characters seems to provide strong evidence that populations from Area 6 have undergone differentiation. However, animals from the whole area have relatively small skulls and may share some common features. We may then interpret Area 6 in several ways:

- a. a region where the apparent existence of common features is an artifact of the categories chosen during the analysis. Area 6 may therefore be harbouring a series of unrecognized units (similar to those of areas 1 to 5). This will only be elucidated when larger samples are available, so that new morphological categories can be chosen.

- b. a region where homogeneity, although not an artifact, is not due to a common gene pool; the common features would be due to environment-determined convergence. Area 6 coincides, coarsely, with the open vegetation domains of Brazil. If convergence is to be accepted, one would have to explain why not all specimens are alike. If the difference could be attributed to different animals using slightly different niches, one would expect the differences to follow some regularity in their distribution among the age-sex classes, something for which there is no evidence.

- c. a region where no speciation has occurred, where the observed common features identify a new unity produced by extensive hybridization among the forms of areas 1 to 5 (all peripheral to area 6).

- d. a region within which there has in fact been some speciation, but whose exclusive characters are less obvious than in the other 5 areas.

I favour an interpretation which includes both c and d. I see area 6 as an area of extensive mixture which may harbour a core

area, based on the following indications:

Hybridization - Some phenotypes observed in this area seem to be transitions to forms of neighbouring core areas. For example, some samples (MG-9, MG-13, BA-4, MG-8) include animals whose cap is thick and bent backwards; this can be seen as a transition towards the flattened cap observed in eastern Bahia (area 3). Also, animals in area 6 seem more prone to having flanks with a mottled appearance than animals in the other areas. The mottled appearance is not similar in different animals, and suggests rather a mixture.

Extensive areas of hybridization - Area 6, as said before, coincides, grossly, with open formation domains, mainly "cerrados" and "caatingas". In these domains, Cebus are restricted to narrow gallery forests. Besides being restricted to a narrow belt along rivers margins, these forests are not so species-rich as the forests in the Atlantic or Amazonian domains. Although I known of no work on the relative quality of these habitats, gallery forests are probably a harsher habitat for primates as they support fewer primate species.

Even relative harshness may have important consequences for gene flow. Endler (1977, p.27) states that in sub-optimal habitats the velocity of dispersal may be higher. In a given period of time, all else being equal, genes of "open formation" populations would be carried over longer distances than those of "forested domains" populations.

Even if gallery forests prove not to be of relatively poor quality (as compared to the continuous forests of the Atlantic domain), the

fact that they are narrow would cause the home range of a "cerrado" troop to stretch over longer distances than that of a "forest" troop of similar size; genes would be carried over longer distances in the same amount of time. Gallery forests in central Brazil are often around 100m wide; assuming a home range of 100 ha for a Cebus troop, a home range for a troop of Cebus would be 10km long in gallery forests, and 1km long in continuous forest. This is assuming that gallery forests are of the same quality as the Atlantic or the Amazonian forest, but, as said before, the gallery forests are probably a relatively poor environment, and the home range size required by a troop in a gallery forest will probably be comparatively larger.

This may partly explain why what I see as a mixture of races spreads over such a vast area in central Brazil, whereas along the Atlantic coastal forest the mixture seems to be more restricted (see, for instance, the small distance that separates areas 3 and 4). The various forms around the "cerrado" might have more easily contacted each other along the "corridors" of gallery forests.

An unclear core area? - If seen as a region of blending of races, the occasional common features between animals from this area could be explained as in "c" above. However, "d" is also possible. A core area of the size of Area 4 could have been missed in central Brazil. Its exclusive characters (one of which would be a very small skull) could only be guessed through the diffuse effect on the hybrids around the core area (e.g. MT9, MT6). It is also possible that, even if the core area had been sampled, its characteristic form would not be as distinct as those of the other core areas , due

to the quicker hybridization in central Brazil.

Are the various tufted forms really races?

Various indications lead me to accept that all forms grade into one another and may eventually blur the pattern of core areas. For instance there are specimens which seem to be intermediates between the forms of adjacent core areas ; such intermediates were found in AM1, Peru-3, BA7, ES7, ES4+5, MG10, MG29, MG11 and MG9 (some indicated in Fig.II.26); also, there seems to be a flank colour gradient between some forms (e.g. from core area 5 to the northwest into core area 6). The relationship between the forms is not, however, clear. Even if I had intermediates between the forms of all adjacent core areas, one could interpret the evidence in other ways. An alternative view would be to admit that these intermediates are not as viable as the core area forms; they would tend to disappear in the long run, and the various forms would reach full species status.

Although it is not unreasonable to consider the forms of the various core areas as races, one might consider Remington's (1968) suggestion that even full species may produce hybrids in the early stages of a secondary contact, simply because during isolation there was no selective pressure for behavioural isolation to be developed between forms. In a morphological study like this no distinction could be made between species hybrids and races hybrids. Only a study of the populations dynamics could provide information about the hybrids' relative fitness. However, if the phenotypes in Area 6 are in fact mixtures of the adjacent core areas forms, the distribution of "mixed" populations is so ample that it makes the

idea of previous full speciation hard to accept.

Refined differentiation models may be formulated when neat clines are recognized, but the present sample did not reveal neat clines. The information concerning the Amazonian region is particularly limiting. The spacing between good series is very large and therefore the isophenes for this region are all very coarse. Although it can be seen that all over Amazonia C.apella share some morphs (e.g. a low sagittal crest, a nitid dorsal stripe), and that Amazonia harbours at least 2 core areas, the relationship between the forms of these two core areas, or between them and those of area 6 (assuming there are no other core areas in between) could not be examined.

The northwestern part of C.apella distribution (Colombia and Venezuela) went completely unsampled, and I do not know whether there are core areas in that region. In this respect it is perhaps relevant to quote Hernandez-Camacho and Cooper's (1976,p.59) more supported opinion: "we remain unconvinced, on the basis of examination of over 120 widely distributed museum specimens, that Cebus apella north of the Amazon from Colombia eastward exhibit phenotypic distinction that would justify the recognition of more than one subspecies throughout this large region". This statement implies that at least two races described for western Amazonia (maranonis Pusch 1941 and magnus Pusch 1941) would have to be synonymized. It is encouraging to see that, when larger samples are examined with a population approach, other observers also tend not to accept previously described forms as separate races.

VARIOUS POSSIBLE PROCESSES BY WHICH THE TUFTED FORMS COULD HAVE EVOLVED

The variables involved in speciation can be combined into countless "explanations" for the observed patterns. Although these "explanations" will remain mere possibilities, unless substantiated by independent evidence, it is interesting to see how the morphological data of Cebus apella fits various models. I will briefly consider four of them:

a) Processes involving geographical isolation of populations:

a1. rivers as geographical barriers to gene flow

a2. isolation due to forest retraction during the Pleistocene

b) Processes which do not involve geographical isolation of populations:

b1. selective pressures on individual populations

b2. distance as a relative barrier to gene flow

a1. Rivers as geographical barriers to gene flow Isolation by physical barriers may provide the set-up for population differentiation. Isolation of populations by rivers, together with the "metachromism" theory, were used by Hershkovitz (1977) to explain the differentiation of various Amazonian tamarins species (Saguinus nigricollis and Saguinus mystax groups).

In the case of Cebus apella there has been some suggestion that rivers may have had some importance in promoting differentiation. Hill (1960) indicated that R.Amazonas, R.São Francisco and R.Paraná separated different races. For the last case the suggestion is

strengthened by field reports by Kuhlhorn (1939, 1943). R.Doce has also been reported to separate different forms of tufted Cebus since Wied (1829), who based the statement on his own field experience and on hunters reports.

In order to examine these suggestions, I compared my samples from opposite margins of each relevant river. If the samples near the margin were too small, I checked the next nearest ones of each side.

R.Doce - I compared the following relevant samples: MG5, MG7, MG10, ES4=5, ES7 (right bank) and ES1=6, ES2, MG4 (left bank). There is a nitid difference between coat colour on each side. Animals on the left bank are reddish (see description for ES2 in Appendix II.5) and have a pointed tuft. The animals in the right hand bank have coats of various shades of brown (often mottled or with a faded appearance), but are not reddish (MG5, MG7, MG4, MG10, ES5), and their tufts do not form a point. This distinction was particularly well illustrated by sample MG4, which included animals from both banks. This evidence seems to suggest that the river does in fact isolate two different populations. However, several animals in the right bank (MG7, ES4, MG10) have caps with an intermediate appearance between the forms further south and those of the left bank (MG7, ES4, MG10). I see this as an evidence that presently there is interbreeding between the populations on both sides, and that the differentiation has not originally arisen because of the river as a geographic barrier.

R.Paraná - Kuhlhorn (1939,1943) indicated that C.apella west of R.Paraná have coats of various shades (yellowish-brown,

greyish-yellow, brown), whereas to the east of the same river they are brownish-black.

From my sample, it seems that there may be some differences between the populations of both sides of the river, but it may not be as clearcut as the literature indicates. SP-24 and MT-12 are one-animal samples from opposite banks of R.Paraná. Both are females, apparently adult. In both animals the flanks are greyish brown, although the animal of the west bank (MT12) seemed to be slightly yellowish, and with the dark parts of tail, limbs and cap of a lighter shade of brown. However, considering samples MT5,MT10 and MT8 (supposedly more similar to MT12) against SP20,SP21 and SP29 (supposedly more similar to SP24), I found that the variation was large and that animals from different sides could not be distinguished with confidence. There was a tendency for animals from the west of R.Paraná to have lighter coloured caps and limbs, but this was not found in all animals.

R.São Francisco - my sample, although small, indicates that there seems to be a noticeable difference between the animals from the left and right banks of this river. However, samples of both sides may be variable, and those to the east do not seem as homogeneous as samples from core area 3. My samples from the banks consisted of an immature male from BA7 (east) and an adult female from BA6 (west). The first one has the colour pattern typical of core area 3 (see Appendix II.5, BA5) and a cap which looks intermediate between those of areas 3 and 4. The animal from BA6 has a very reddish brown coat and a forward/sideways cap. The next nearest samples are BA4 (to the west) and BA2 (to the east), both quite far from the river. BA2

is a 3 animals sample, and BA4 is a 11-animal sample. In BA2 at least two of the animals had coats like that of BA7, their caps being either an irregular mixture of yellowish and brown patches, or reminiscent of the cap typical of core area 3. In BA4 the coat was of various shades of light brown, occasionally with lighter shoulders. Their caps were variable, generally thicker and more upward projecting than the caps of core area 3, but had in common with these a wide band of lighter-coloured hairs between eyes and cap, and also a tendency to be bent backwards.

R.Amazonas - I was not able to detect any striking difference between the animals from the north and south banks of R.Amazonas. I examined two series of samples: AM2+3+4 (north) against AM5 (south), both localities being at the river margin, and then PA2+5 (north) against PA9, PA10 and PA13+14+15 (south). All animals had coats of varying shades of brown with lighter shoulders, and the caps varied from completely tuftless to caps with two high erect tufts.

There is therefore some indication of difference between the populations from opposite banks of R.Doce, R.São Francisco and R.Paraná. However, in other rivers of comparable (or larger) width there is not such difference: no consistent difference was found between the animals from the northern and southern banks of the low Amazon, or between those of western and eastern banks of R.Tapajós. Both are very wide rivers and isolation of populations in opposite banks might be expected. It seems that if isolation by rivers has had some effect in the differentiation within the species, this mechanism certainly does not explain the existence of all forms. Those of areas 3 and 4, for instance, are not separated by any major

river.

Even if in some cases rivers separate forms which are on average different, this does not mean that the river barrier was necessary for the differentiation to occur. The river might happen to be between expanding populations of previously differentiated forms.

a2. Isolation due to forest retraction during the Pleistocene

Refuges are areas where environmental conditions are favourable to the survival of the organism in question; they are separated by extensive less suitable areas where extinction is likely (Brown and Ab'Saber 1979). Refuges have been postulated to have formed during climatic oscillations associated with the Quaternary glaciations. During a glaciation the sea level lowered, ocean currents changed their location and this affected the climate on the continents. During glaciation, the climate in South America became dry and cold, whereas it was warmer and damper during inter glacial periods. The alternation of the two types of climates would have corresponded to cycles of expansion/retraction of forests. During the dry periods savannas would have expanded greatly, isolating forest species in a number of small refuges, where presumably they started differentiating. The last dry spell would have happened 13000 to 18000 years b.p. (Ab'Saber 1977). Subsequently, the various differentiated forms would have come together. This process has been invoked to explain the high diversity of organisms in the superficially homogeneous forests of the Neotropics (Vanzolini 1973, Simpson & Haffer 1978).

Several biological facts seem to support this model. These

include the geographical distribution of bird species (Haffer 1969), sub specific morphological characters in lizards (Vanzolini and Williams 1970), butterfly species (Brown et al. 1974) and tree species (Prance 1974). Different organisms repeatedly indicate that certain areas (refuges) are probable sites of speciation.

The refuge model has become fashionable. Many patterns have been explained by it. It should be said, however, that some of the biological evidence for the existence of refuges is rather unsatisfactory. Since each species may respond to isolation and habitat changes in its own unique way, an area which is a refuge for one species may not be so for another (Oren 1979). This has been used as an explanation as to why different studies do not yield the same number and the same location of refuges, and because of it all postulated refuges tend to be accepted. The difficulty arises when researchers use refuges from independent studies, to explain the particular distribution they have in hand. There are so many postulated refuges that almost any pattern could be in part explained by ascribing the various forms to one of the nearest refuges. This is a superficial procedure; it does not provide additional evidence for the model. If bits of information do not fit the already described refugia, either they are explained otherwise, or new refugia are proposed. In this exercise of ascribing forms to refuges, different researchers may favour different interpretations. For example, the same elements (subspecies of Callithrix jacchus) are postulated to have evolved in different ways and sites by Kinzey (1980) and by Cerqueira Silva (1980).

Discounting the misuses, there is evidence supporting the idea that

isolation in refugia has been an important factor in the diversification of the Neotropical biota. Several types of organisms consistently indicate certain areas as being occupied by endemic forms. Taxonomic studies at the subspecific level indicate intergradation in areas where there seems to be no ecological barrier. More direct evidence is provided by geomorphological, climatological, pedological and palynological studies; these indicate that during the Quaternary there were indeed climatic and vegetational cyclic changes in the Neotropics, and that the last alteration involved a transition from dry to humid (present) conditions. (Van der Hammen 1974, Absy 1979, Ab'Saber 1977, Bigarella & Ab'Saber 1961). Unfortunately this type of data is restricted to a few localities, so it is not possible to draw accurate maps of the distribution of forests during the dry spells. Some researchers have tried to predict the location of refuges on the basis of present day rainfall patterns. This is reasonable because there is a relationship between the amount and dispersion of annual rainfall and the local type of vegetation. Haffer (1969), indicated a number of areas (which nowadays have high and regular rainfall) as having been refuges during past dry/cold spells. This prediction is based on the assumption that the present geographical pattern of rainfall has remained unchanged. The refuge areas as suggested by the rainfall matched Haffer's data on bird distribution well. Can it also account for Cebus morphological differentiation?

Fig. II.28A gives the modern isohyets for tropical South America (from Simpson and Haffer 1978). According to those authors, the areas with at least 3000mm/year would have supported humid evergreen forests during an arid phase (shaded areas in the map).

Since those authors were mainly concerned with the Amazonian region, that part of the map is more detailed than the Southeastern part, for which I used another map (Fig. II.28B)

Do the areas of high rainfall correspond to the areas of character stability in tufted Cebus? My samples do not cover the whole of Amazonia, but it can be seen that the two Amazonian "core areas" (1 and 2) correspond to areas of relatively high rainfall. Core area 2 coincides with one of the two regions of highest rainfall in the Amazonia; core area 1 does not. Nevertheless, core area 1 is near the cell of 3000mm high rainfall north of R.Jurua and might be overlapping with it; unfortunately, as I have no samples from the region north of R.Jurua, the overlap cannot be checked. An association between core area 1 and the rain cell north of R.Juruá is possible, but requires samples from more localities.

Outside Amazonia the rainfall is much lower, with the isohyets above 2000mm/year restricted to relatively small areas in the mountainous regions. Do the non-Amazonian core areas fit this picture? The three core areas where animals have uniform phenotypes are areas 3,4 and 5. Each of these is either on or near a region of high (although not necessarily highest) rainfall. The more controversial core area 6 is very large and crosses several isohyets, none of which is, however, as high as those found in the forested regions.

In areas where the rainfall is not very high, it is important to consider the distribution of rain and the duration of the dry season. Fig.II.29A shows the length of the annual dry period for the Southeast of S.America. It is similar to II.28B, but it shows that only along the coast are there regions with no dry period. and that these do not necessarily correspond to the areas with highest

Fig. II.28 - Total annual rainfall (in millimeters) in (A) northern and central South America and (B) southeastern Brazil.

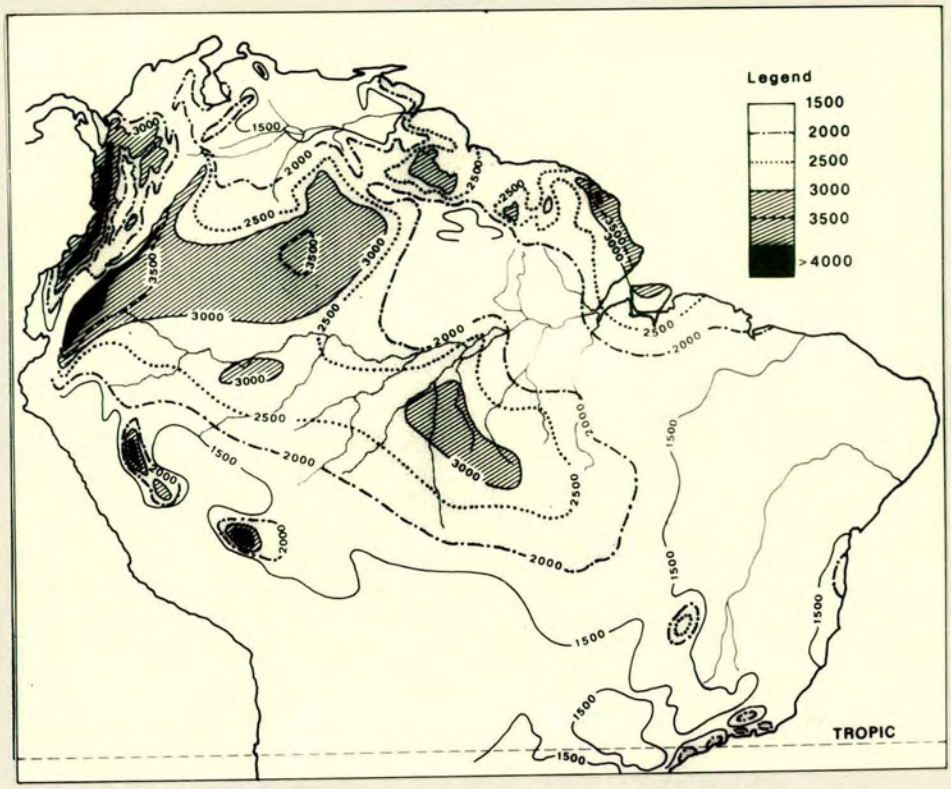
(A) - from Simpson and Haffer (1978)

(B) - adapted from Nimer (1977)

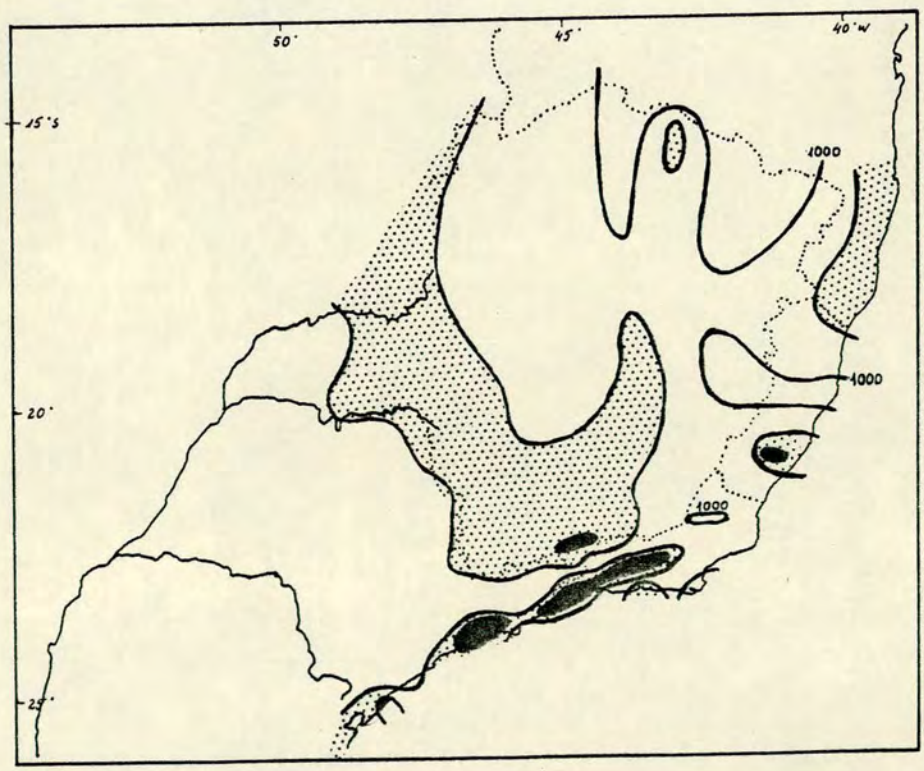
For (B), the code is:

> 2000 mm	black areas
1500 - 2000 mm	dotted areas
1000 - 1500 mm	white areas
< 1000 mm	white areas limited by isohyet

A)


Legend
1500
2000
2500
3000
3500
>4000
TROPIC

B)


50°
45°
40°W
15°S
20°
25°
1000
1000
1000

rainfall. There are five such regions. Two of them are associated with core areas (3 and 5). Although it is tempting to associate core area 4 with the intervening region of high rainfall, core area 4 is in fact located to the north of it. The region of high humidity corresponds to the Caparaó mountain range, to the south of R.Doce, and core area 4 corresponds to the Aymorés mountain range, north of the same river; the Aymorés range does not show at present a particular high rainfall, and is subject to some dryness. However, the indications are that this region did not dry during the Pleistocene (Vanzolini and Williams, 1970). Unless the spot of high rainfall shifted positions since the Pleistocene, it seems that at least in the case of core area 4, refuges are unlikely to be the explanation for the differentiation of the local form.

Core areas along the coast have also been recognized by other researchers, e.g. by Cerqueira Silva (1980), in his study of the morphological differentiation of Didelphis (Marsupialia)(see Fig. II.29B). Although the methods used by Cerqueira-Silva (and also the collecting localities) were different from mine, there are several interesting matching features in our results:

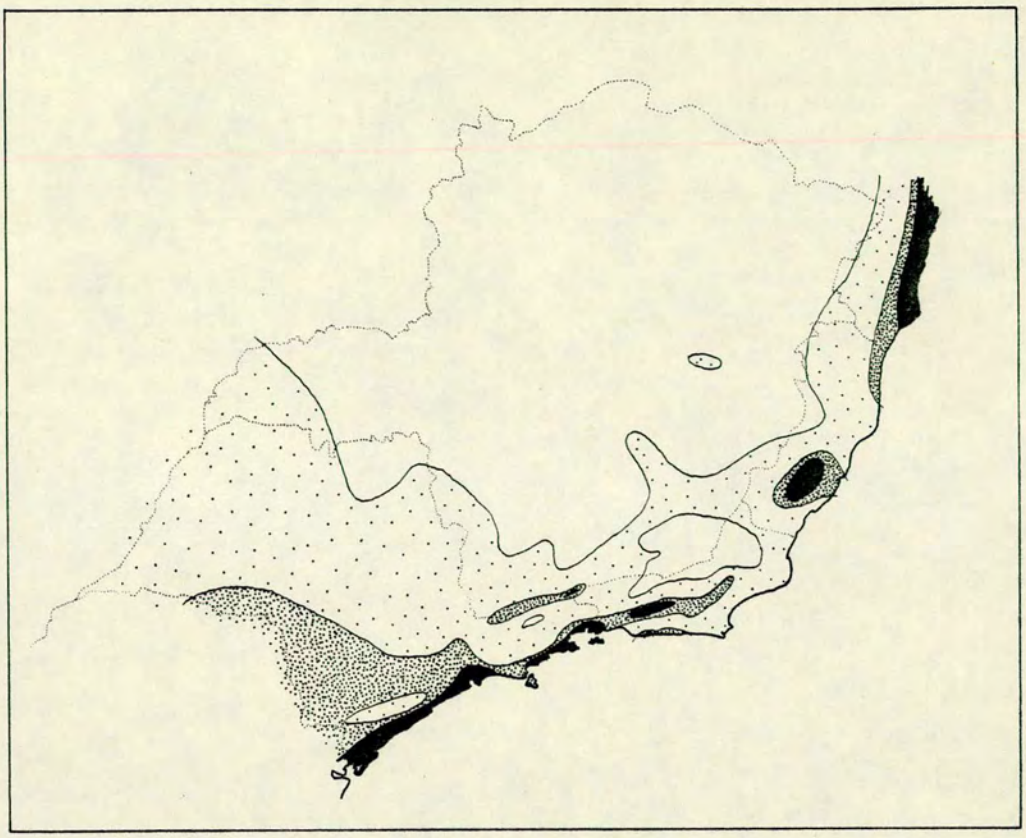
- the region of break between my areas 3 and 4 has a counterpart in the similarity indexes within C.Silva's area A, where Ilhéus (my area 3) can be distinguished from E.Santo (my area 4)
- the region of break between my areas 4 and 5 corresponds in C.Silva's results to an independent core area; I did not recognize an independent core area in that region, but to the extent that it has more affinities with core area 6 than with either 4 or 5, it matches C.Silva's pattern.
- C.Silva's area D encompasses my area 5

Fig. II.29 (A) - Duration of dry periods in Southeastern Brazil (adapted from Nimer 1977).

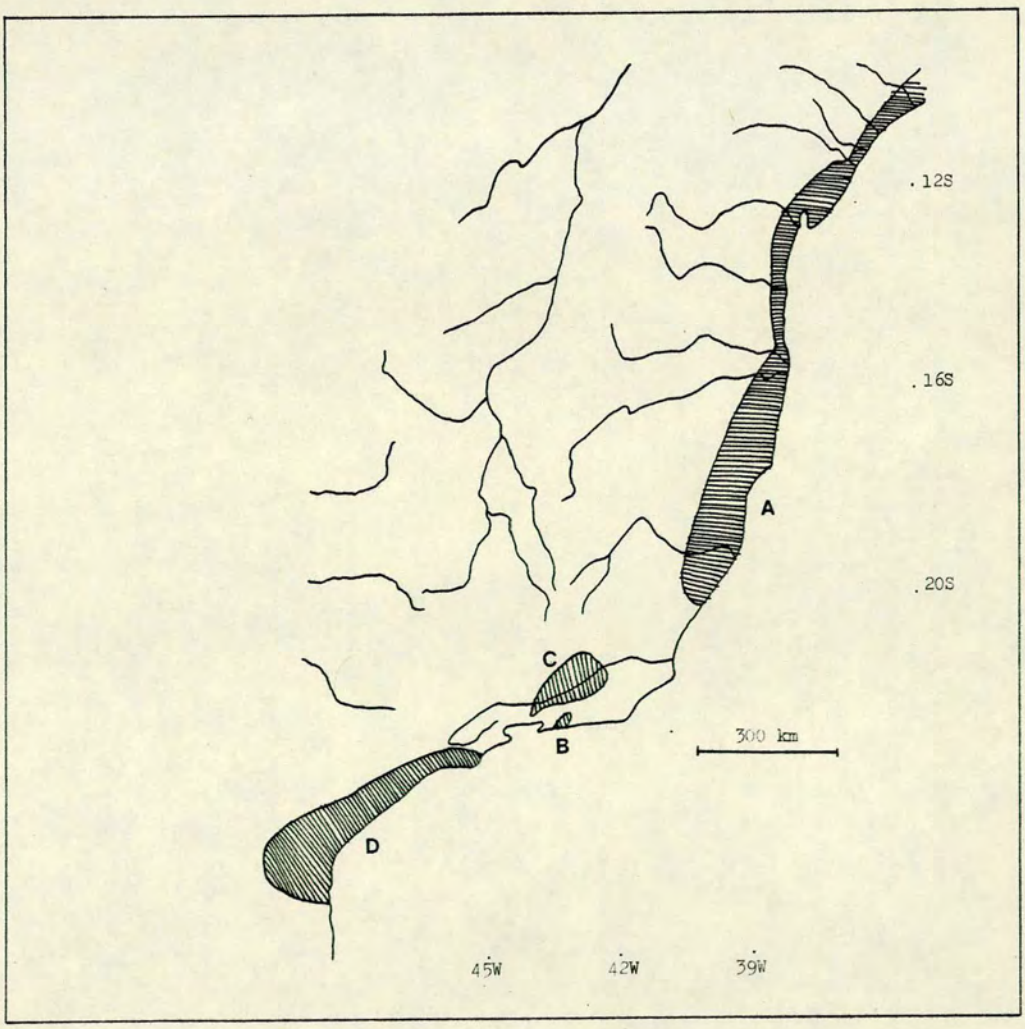
Black areas - no dry periods
Densely dotted areas - only a sub-drought
Sparsely dotted areas - 1 to 3 dry months
White areas - 4 to 6 dry months

(B) - Core areas of southeastern Brazil as suggested by skull measurements of Didelphis marsupialis (copied from Cerqueira Silva 1980).

A)



B)



The results of this study, except maybe that of core area 4, do not contradict the refuge model. Even if it is accepted that the various tufted forms evolved through isolation in Pleistocene refuges, that does not tell anything about the evolutionary sequence. A simple sequence would be the isolation of populations from a stock occupying the whole of the present day's distribution when the first glaciation occurred. In this case, the difference between races might have been emphasized at each glaciation, if the refuges were repeatedly in the same areas, as suggested by Vanzolini (1973, p.256). However, the evolutionary sequence may have been more complex, with differentiation being followed by colonisation, new isolation, etc..

b1. selective pressure on individual populations

Speciation does not require the strict allopatry which has been the premise in a1 and a2 (Endler 1977, Benson 1979, Colinvaux 1979). Geographical patterns could also be due to selection gradients along ecological clines, environmental discontinuities, or gradual modification of climate and biotic communities. Even in a superficially homogeneous, continuous forest, there may be different sub-habitats, sub-systems of associated organisms and presumably a complex interaction of selective pressures. These might be directly responsible for the development of recognizable units, correlated across taxonomic groups.

The resulting pattern would be similar to that of coalesced refuges, even if they did not exist as separate entities.

Could such process account for the existence of the various tufted forms? Some of the core areas (2, 3 and 5) coincide with

regions where there is high rainfall and no dry period. These factors might be important in determining particular environmental pressures resulting in a distinct and uniform local population. The coincidence between core areas and regions with no dry period does not, however, hold in all cases (core areas 4 and 6) and, even in the cases where there is a coincidence, the core areas do not accompany the isohyets very closely. I do not believe that the distribution of morphs in the tufted Cebus is a product of selective pressure on individual populations because in most localities there is huge variation in all examined characters. However, alternative a2 cannot be discarded until the environmental conditions in the various localities are individually assessed and checked against intrapopulation variability.

b2. distance as a relative barrier for gene flow

Endler (1977) has demonstrated that there can be differentiation not only in the absence of physical barriers to gene flow, but also in the absence of environmental heterogeneity. This may happen because isolation by distance can be just as important in promoting geographic divergence and speciation. The clines evolved through this process may remain relatively stable (geographically) over hundreds of generations and might be taken as the product of secondary contact. In fact, according to Endler, we can only tell secondary clines apart from "primary clines" (clines evolved in the absence of barriers) if we get certain information about the zone of intergradation within a few hundred generations of secondary contact. Such information refers to the relative and absolute fitness of hybrids, velocity of dispersal, population dynamics,

etc.. This type of information is not (and may never be) available; Endler's suggestion may therefore remain an untested possibility. It is, nevertheless, important to mention it here, as it prevents one from unduly accepting other equally unproven explanations. Also, the possibility remains that more than one mechanism may have acted jointly to produce the observed pattern. For instance, Brown and Ab'Saber (1979, p.2) indicated that some aspects of the available biological data (such as biotic endemism) seem to be better explained by past climatic changes, while others (such as species richness) are more related to present-day conditions.

THE RELATIONSHIP BETWEEN THE VARIOUS FORMS OF TUFTED *CEBUS*

The relatedness of forms is determined by the speciation sequence. As seen in the previous section, there could be a number of possible ways in which the presently observed pattern was formed; this makes it impossible to deduce the relatedness between forms from their evolutionary story. Nevertheless, the relatedness can be inferred from the animals' morphological characters. These do not always reflect the real relatedness between forms, because convergence in some characters may suggest a false relatedness between otherwise different forms. The risk of using such unrepresentative characters can be reduced by using information from more than one character system. In this study only three systems could be sampled: cranial size/shape, pelage colour and cap shape.

I discarded pelage colour as a similarity-indicating

character; although one can compare between different grades of the same colour, it is problematical to decide whether a red animal is more similar to a black one than to a brown one. Hershkovitz (1977) suggested that mammal hairs tend to follow a fixed sequence of saturation/bleaching; if the process is real, it would allow the tracing of certain lineages through their colours; however, this is based on the assumption that the sequence can always be observed, which means that selection does not act particularly strongly on either phase. This is unlikely. The most light-coloured tufted Cebus are found in the areas of more open habitat and the most dark-coloured ones are found in southern (cooler) areas, which suggest that pelage colour is important in the animals' fitness. For Alouatta, Thorington et al. (1979) also suggested that variation in pelage colour was an adaptation to different thermal environments. One would expect convergence in pelage colour to be frequent. A further complication is the possibility that Cebus pelage colour changes with season (Kuhlhorn 1939, Rengger 1830), age (Rengger 1830), diet (Fiennes et al. 1973), or other unknown causes (Cabrera 1924). There are too many variables affecting pelage colour for it to be considered a safe indicator of phylogenetic relationships.

Affinities in skull characters can be examined in the results of the multivariate analysis already described (see Figs. II.15 and I.16).

Two of the six distinguishable regions could not be included in the comparison because they were not represented by adequate skull samples. For the others, the similarity levels in Fig.II.15 suggest:

Males - A higher similarity was found between animals from parts of region 6 and those of region 4 than among all localities of region 6 (animals from MT6 being particularly different). Animals from reg.6 and reg.4 are quite different from those of region 1 and 5; it would also seem that some localities from reg.1 are more similar to those of reg.5 than they are to other localities of reg.1 itself.

Females - Individuals from some localities in region 6 are more similar to animals from reg. 4 than they are to those of some localities (PA13 and MT9) within reg.6 itself. Animals from these two regions are quite different from animals from reg. 1 or reg.5. It would also seem that reg.1 and reg.5 are more similar between themselves than parts of reg.6 are.

It is difficult to believe that animals so far apart as those of Reg.1 and 5 could be more related than animals from adjacent localities. This may be a reflection of the importance of factor 1 (size factor) in the multivariate analysis - animals in reg.1 and 5 being very big, they were associated as being more related. The big size of the skull may be a convergence. On the other hand, the heterogeneity within reg.6 is not a surprise. If reg.6 is indeed an area of extensive mixture, its animals should show affinities with those of the nearest core areas. The fact that MT6 and MT13 appear as slightly different may be an indication of an unclear core area, but the indication is too weak to allow conclusions.

Although the form and size of tufts is quite variable, there are some aspects of the cap shape (particularly the forehead pattern) which suggest some affinities. Since the primitive Cebus species are tuftless (as suggested by the work of Torres de

Caballero et al. 1976), the untufted Cebus apella forms (Reg. 1) are probably the most primitive ones within the species. These are Amazonian in distribution, just as the other untufted species; this indicates Amazonia as the most likely origin for the ancestor of the tufted animals. The forehead pattern in "V" indicates affinity between Reg.1 and Reg.2. Animals from Reg.1 are also very similar to those of Bolivia. I do not have good samples from the south and southeast of this area. Crespo (1950) stated that only one form occupies all of Paraguay, the eastern and southern parts of Bolivia and most of Mato Grosso State in Brazil; although he considered it to be different from the form of the "llanuras" of Bolivia, if this whole area is homogeneous then the form is a gradation between tufted and untufted (my data from MT). In all recognized regions outside Amazonia, the animals have in common the conspicuousness of tufts in adult age (even though the shape of the tufts may vary considerably). Reg.3 and 4 have also in common the wide band on the forehead and the fact that the tufts are not restricted to a narrow frontal area. It seems, on the basis of this evidence, that two blocks can be recognized: one Amazonian (Reg.1 and Reg.2) and one along the Atlantic coast (Regs. 3, 4 and 5). The relationship between the two is not clear. The original stock was probably Amazonian; because all the animals in the coastal area have tufts, they might have originated from populations already differentiated in Reg.2. Without more evidence, it is only speculative to imagine the relationship between the two blocks.

SUMMARY

1. Six "core areas" are recognized where a number of characters show relative stability. For five of these "core areas" a typical phenotype is easily distinguished. This is not the case for the sixth one, which seems not to be strictly comparable to the first five.

2. If seen as a site of speciation, the population of each "core area" can be considered a different race, with the forms present between core areas seen as intergradations.

3. It is difficult to indicate the evolutionary mechanism and sequence that produced the present distribution of Cebus forms. There are many possible explanations for the observed pattern; some of them are discussed.

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-Secretaria Especial do Meio Ambiente: José Pedro Costa (Juréia Reserve)

-Private owners: Suzanna Campos, Roberto Melillo and the late Mário Cintra Leite, and also Pedro Neumann and family.

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- British Museum, London : Prudence Napier
- Museu de Zoologia da U.S.P., São Paulo : Mário de Vivo, Eleonora Trajano and Nelson Gomes
- Museu Goeldi, Belém : Fernando Novaes

- Museu Nacional, Rio de Janeiro : Francisco Cruz, Sérgio Vaz, Regina Correa.

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REFERENCES

AB'SABER, A.N. (1977a) Os domínios morfoclimáticos na América do Sul. Geomorfologia-52. Instituto de Geografia, Universidade de São Paulo, São Paulo.

AB'SABER, A.N. (1977b) Espacos ocupados pela expansao dos climas secos na America do Sul, por ocasiao dos periodos glaciais quaternarios. Paleoclimas 3. Instituto de Geografia da Universidade de Sao Paulo, Sao Paulo.

ABSY, M.L. (1979) Quaternary palinological studies in the Amazon basin. Fifth Int. Assoc. Trop. Biol. Symp., La Guaira, Venezuela.

AGUIRRE, A.C. (1971) O mono Brachyteles arachnoides (E.Geoffroy). Academia Brasileira de Ciências, Rio de Janeiro.

ALONSO, C. (in prep) (manuscript)

ALONSO, M.T.A. (1977) Vegetação. pp.91-118 IN Geografia do Brasil, (Vol.3, Região Sudeste) Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

ANUÁRIO ASTRONÔMICO (1975) Instituto Astronômico e Geofísico, Universidade de São Paulo, São Paulo, 182pp.

AUBREVILLE, A. (1961) Étude écologique des principales formations végétales du Brésil. U.N.E.S.C.O and Centre National de la Recherche Scientifique, Nogent-sur-Marne.

AUDEBERT, J.B. (1797) Histoire naturelle des singes et des makis (8eme). Desray, Paris.

ÁVILA-PIRES, F.D. (1965) The type specimens of Brazilian mammals collected by Prince Maximilian zu Wied. American Museum Novitates 2209: 1-21.

AYRES, J.M. (1981) Observações preliminares sobre a ecologia e o comportamento social dos cuxiús (Chiropotes satanas e Chiropotes albinasus). Unpublished MSc thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus.

AYRES, J.M. (1983) Conservation of primates in Brazilian Amazonia: problems and strategies. Pp. 2-33 IN Proceedings of the Symposium on the conservation of primates and their habitats (24-25 September 1982, Leicester), Vol.I, Vaughan Papers N.31,Univ.Leicester.

AYRES, J.M. and R.BEST (1979) Estratégias para a conservação da fauna amazônica. Supl. Acta Amazonica 9 (4): 81-101.

AYRES, J.M. and K. MILTON (1981) Levantamento de primatas no rio Tapajós. Boletim do Museu Paranaense Emílio Goeldi. Série Zoologia 111: 1-13.

AZARA, F. de (1809) Voyages dans l'Amérique Méridionale depuis 1781 jusqu'en 1801.....[french version of an older spanish original]. Dentu, Paris.

BALDWIN, J.D. and J.I. BALDWIN (1972) The ecology and behavior of squirrel monkeys (Saimiri oerstedi) in a natural forest in Western Panama. Folia primatol. 18: 161-184.

BALDWIN, J.D. and J.I. BALDWIN (1977) Observations on Cebus capucinus in Southwestern Panama. Primates 18 (4): 937-941.

BATAGLIA, O.C., J.P.F.TEIXEIRA, P.R.FURLANI, A.M.C.FURLANI and J.R.GALLO (1978). Análise química de plantas. Circular n.87. Instituto Agronômico. Secretaria da Agricultura, Estado de São Paulo, 31 pp.

BENSON, W.W. (1979) Alternative models for infrageneric

diversification in the humid tropics. Fifth Int. Assoc. Trop. Biol. Symp., La Guaira, Venezuela.
BIGARELLA, J.J. and A.N. AB'SABER (1961) Quadro provisório dos fatos sedimentológicos, morfoclimáticos e paleoclimáticos na Serra do Mar paranaense e catarinense. Bol. Paranaense de Geografia 2/5. Curitiba.
BRANCH, L.C. (1979) Primates of the Amazon (Tapajós) National Park - a final report. Report presented to Instituto Brasileiro de Desenvolvimento Florestal - DN.
BRANCH, L.C. (in prep) Seasonal and habitat differences in the abundance of primates in the Amazon (Tapajós) National Park, Brasil.
BRASIL (1972) Carta do Brasil ao milionésimo, Ministério do Planejamento e Coordenação Geral, e Fundação Instituto Brasileiro de Geografia e Estatística.
BRISSON, M.J. (1762) Regnum animale in Classes IX distributum ... (Editio altera auctior). Lugduni Batavorum.
BRONZINI, E. (1949) [a personnal communication from Zoological Garden/Rome, to Gray (1954)]
BROWN, K.S. and A. AB'SABER (1979) Ice-age forest refuges and evolution in the neotropics, correlation of paleoclimatological, geomorphological and pedological data with modern biological endemism. Paleoclimas 5. Instituto de Geografia, Universidade de São Paulo, São Paulo.
BROWN, K.S., J.R.G.TURNER and P.M.SHEPPARD (1974) Quaternary forest refugia in tropical America: evidence from race formation in Heliconius butterflies. Proc. Roy. Soc. B 187: 369-378.
BUFFON, G.L.L. (1767) Histoire naturelle générale et particulière, avec la description du cabinet du roi, Tome 15. Imprimerie Royale, Paris.
CABRERA, A. (1924) Sobre el cambio de coloración en un mono del género Cebus. Boletin de la Real Sociedad Española de Historia Natural 24: 130-131.
CABRERA, A. (1917) Notas sobre el género Cebus. Revta. R. Acad. Cienc.Exact.Fis.Nat.Madr. 16 (15): 221-244.
CARPENTER, C.R. (1934) A field study of the behavior and social relations of howling monkeys. Comp.Psychol.Monogr. 10 (48): 1-168.
CARPENTER, C.R. (1965) The howlers of Barro Colorado Island. Pp 250-291 IN Primate Behavior, I.DeVore ED., Holt, Rinehart & Winston, New York.
CAUSEY, O.R., H.W.LAEMMERT,Jr. and G.S.HAYES (1948) The home range of Brazilian Cebus monkeys in a region of small residual forest. Amer. J.Hyg. 47: 304-314.
CERQUEIRA-SILVA, R. (1980) A study of neotropical Didelphis (Mammalia, Polyprotodontia, Didelphidae). PhD thesis, University of London.
CESAR, O. (in prep).
CHALMERS, N. (1979) Social behaviour in primates. E.Arnold, London.
CHIVERS, D.J. (1969) On the daily behaviour and spacing of howling monkey groups. Folia primat. 10: 48-102.
CHIVERS, D.J. and W. LANE-PETTER EDS. (1978) Recents Advances in Primatology, Vol.2 - Conservation. Academic Press, London.
COIMBRA-FILHO, A. (1976) Leontopithecus rosalia chrysopygus (Mikan,1823), o mico-leão do Estado de São Paulo

(Callitrichidae, Primates). Silvic. S.Paulo 10: 1-36.
COIMBRA-FILHO, A. (1978) Natural shelters of Leontopithecus rosalia and some ecological implications (Callitrichidae: Primates) IN Biology and conservation of the Callitrichidae, D.G.Kleiman ED., Smithsonian Institution Press, Washington D.C.
COIMBRA-FILHO, A. and R. MITTERMEIER (1973) Distribution and ecology of genus Leontopithecus Lesson 1840 in Brasil. Primates 14: 47-66.
COIMBRA-FILHO, A. and R.MITTERMEIER (1976) Exudate-eating and tree-gouging in marmosets. Nature 262 (5569): 630.
COIMBRA-FILHO, A. and R. MITTERMEIER (1977) Conservation of the Brazilian lion tamarins (Leontopithecus rosalia) IN P.Rainier and G. Bourne EDS. (1977)
COIMBRA-FILHO, A. and R.MITTERMEIER (1978) Tree gouging, exudate-eating and the "short-tusked" condition in Callithrix and Cebuella. Pp. 105-115 IN Biology and Conservation of the Callitrichidae, D.G. Kleiman ED., Smithsonian Institution Press, Washington D.C.
COIMBRA-FILHO, A., R.MITTERMEIER and I.CONSTABLE (1981) Callithrix flaviceps (Thomas 1903) recorded from Minas Gerais, Brazil (Callitrichidae, Primates). Rev.Bras.Biol. 41 (1): 141-147.
COLINVAUX, P. (1979) The Ice-age Amazon. Nature 278: 399-400.
CRESPO, J.A. (1950) Notas sobre el habitat del "cai" en el norte de Salta. Boletín de la Oficina Sanitaria Panamericana 7: 711-714.
CUVIER, F. (1819) [parts not numbered] IN Geoffroy Saint-Hilaire and F.Cuvier (1824)
CUVIER, F. (1820) [parts not numbered] IN Geoffroy Saint Hilaire and F.Cuvier (1824)
DEFLER, T.R. (1979A) On the ecology and behavior of Cebus albifrons in Eastern Colombia: I. Ecology. Primates 20 (4): 475-490.
DEFLER, T.R. (1979B) On the ecology and behavior of Cebus albifrons in Eastern Colombia: II. Behavior. Primates 20 (4): 491-502.
DELLA SERRA, O. (1950) Sobre as variações das asas do vômer nos macacos do gênero Cebus. Papéis Avulsos do Departamento de Zoologia 9 (23): 351-359.
DUBOIS, M., K.A.GILLES, J.K.HAMILTON, P.A.REBERS and F.SMITH (1956) Colorimetric method for determination of sugars and related substances. Anal.Chem. 28: 350-356.
DURHAM, N.M. (1975) Some ecological, distributional and group behavioral features of Atelinae in Southern Peru: with comments on interspecific relations. Pp. 87-101 IN Socioecology and Psychology of Primates, R.H.Tuttle ED., Mouton, The Hague.
EDWARDS, G. (1758) Gleanings of Natural History .... (Part I). Printed for the author, London.
EISENBERG, J., W. DITTUS, T. FLEMING, K. GREEN, T. STRUHSAKER and R.THORINGTON (Subcommittee on Conservation of Natural Populations, National Research Council) (1981) Techniques for the study of primate population ecology. National Academy Press, Washington, D.C.
ELIAS, M.R. (1977) Relative maturity of Cebus and squirrel monkeys at birth and during infancy. Developmental Psychobiology 10 (6): 519-528.
ELLIOT, D.G. (1910) Descriptions of new species of monkeys of the genera Galago, Cebus, Alouatta and Cercopithecus. Ann. Mag. nat. Hist. 8 (5) : 77-83.

ELLIOT, D.G. (1913) A review of the primates. Vols. I and II. Am. Mus. nat. Hist. Monogr., New York.
ENDLER, J.A. (1977) Geographic variation, speciation, and clines. Monographs in population biology 10. Princeton University Press. Princeton, New Jersey.
FEARNSIDE, P.M. (1982) Deforestation in the Brazilian Amazon: how fast is it occurring? Interciencia 7 (2): 82-88.
FIENNES, R.N.T-W-, A.J.SINCLAIR and M.A.CRAWFORD (1973) Essential fatty acid studies in primates. Linolenic acid requirements of capuchins. J.med.Prim. 2: 155-169.
FISCHER, J.B. (1829) Synopsis mammalium. J.G.Cotta, Stuttgardiae [apud Napier 1976]
FONSECA,G.A.B., T.LACHER, C.ALVES JR and B.MAGALHÃES-CASTRO (1980) Some ecological aspects of free-living black tufted ear marmoset (Callithrix jacchus penicillata). Abstracts of the VIII Intern. Congr. of Primatology 3(2): 197.
FRAGASZY, D.M. (1980) Choice of travel paths by squirrel and titi monkeys. Abstracts of the VIII Intern. Congr. of Primatology 3(2): 198.
FRAGASZY, D.M. and W.A.MASON (1978) Response to novelty in Saimiri and Callicebus - influence of social context. Primates 19 (2): 311-331
FREESE, C.H. and J.R. OPPENHEIMER (1981) The capuchin monkeys, genus Cebus. Pp 331-390 IN Ecology and behavior of neotropical primates, Vol.1, A.F.Coimbra Filho and R.Mittermeier EDS., Academia Brasileira de Ciências, Rio de Janeiro.
FREESE,C., P.G.HELTNE, N.CASTRO and G.WHITESIDES (in prep) Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distribution.
GABRIEL, K.R. and R.R.SOKAL(1969) A new statistical approach to geographic variation analysis. Systematic Zoology 18: 259-278.
GALLO, J.R., J.P.F.TEIXEIRA, D.S.SPOLADORE, T.IGUE and L.T. DE MIRANDA (1976) Influência da adubação nas relações entre constituintes químicos dos grãos, dos grãos e das folhas, e a produção de milho. Bragantia 35 (36): 413-432.
GAUTIER, J.P. & A.GAUTIER-HION (1969) Les associations polyspecifiques chez les Cercopithecidae du Gabon. La Terre et la Vie 23: 164-201.
GEOFFROY SAINT-HILAIRE,[E] (1812) Tableau des quadrumanes. Annls. Mus. hist. nat. Paris 19: 85-122.
GEOFFROY SAINT-HILAIRE, E. and F.CUVIER (1824) Histoire naturelle des mammifères, avec des figures originales, coloriées, dessinées d'aprés des animaux vivans. Tome I. Muséum d'Histoire Naturelle, Paris.
GEOFFROY SAINT-HILAIRE, I. (1850) Note sur plusieurs espèces nouvelles des mammifères, de l'ordre des Primates. Compte Rendu des Seances de l'académie des Sciences 31, n.27: 873-876
GEOFFROY SAINT-HILAIRE, I. (1851) Catalogue méthodique de la collection des mammifères, de la collection des oiseaux et des collections annexes. Gide and Baudry, Paris.
GILMORE, R.M. (1943) Mammalogy in an epidemiological study of jungle yellow fever in Brazil. J.Mamm. 24: 144-162.
GOLDFUSS, G.A. (1809) Vergleichende naturbeschreibung Saugethiere. Abth 1. Erlangen [apud Napier 1976]
GRAY, J.E. (1865) Notices of some apparently undescribed species of Sapajous (Cebus) in the collection of the British Museum.

Proc.zool.Soc.London (1865) pp 824-828.
GRAY, A.P. (1954) Mammalian hybrids. 1st.edition. Tech.Comm.Bureau of Animal Breeding and Genetics, Edinburgh.
GRAY, A.P. (1972) Mammalian hybrids. 2nd.(revised) edition. Tech. Comm.Bureau of Animal Breeding and Genetics n.10, Farnham Royal, Slough.
HAFFER, J. (1969) Speciation in Amazonian forest birds. Science 165 (3889): 131-137.
HELTNE, P. (1976) Introduction IN R.Thorington and P.Heltne EDS. (1976)
HERNANDEZ-CAMACHO, J. and R. COOPER (1976) The non-human primates of Colombia. pp 35-69 IN R.Thorington and P.Heltne EDS. (1976)
HERSHKOVITZ, P. (1949) Mammals of Northern Colombia. Preliminary report n.4 (Primates) with taxonomic revisions of some forms. Proc.U.S.Nat. Mus. 98: 323-427.
HERSHKOVITZ, P. (1955) Notes on American monkeys of the genus Cebus. J.Mamm. 36: 449-452.
HERSHKOVITZ, P. (1959) The scientific names of the species of capuchin monkeys (Cebus Erxleben) Proceedings of the Biological Society of Washington 72: 1-3.
HERSHKOVITZ, P. (1975) Comments on the taxonomy of Brazilian marmosets (Callithrix, Callitrichidae). Folia primat. 24: 137-172.
HERSHKOVITZ, P. (1977) Living New World monkeys (Platyrrhini) Vol.1 University of Chicago Press.
HILL, W.C.O. (1960) Primates - comparative anatomy and taxonomy. Vol.IV - Cebidae, Part A. Edinburgh University Press (1964 printing)
HILL, W.C.O. (1962) Primates - comparative anatomy and taxonomy. Vol.V - Cebidae, Part B. Edinburgh University Press.
HLADIK, A. (1978) Phenology of leaf production in a forest of Gabon: distribution and composition of food for folivores. Pp. 51-71 IN The ecology of arboreal folivores, G.G.Montogomery ED., Smithsonian Institution, Washington, D.C.
HLADIK, C.M. (1978) Adaptive strategies of primates in relation to leaf-eating. Pp. 373-395 IN The ecology of arboreal folivores, G.G.Montgomery ED., Smithsonian Institution, Washington, D.C.
HLADIK, A. and C.M.HLADIK (1969) Rapports trophiques entre végétation et primates dans la forêt de Barro Colorado (Panama). Terre et Vie XXIII (1): 27-117.
HLADIK, C.M., A.HLADIK, J.BOUSET, P.VALDEBOUZE, G.VIROBEN and J.DELORT-LAVAL (1971) Le régime alimentaire des Primates de Barro-Colorado (Panama). Folia primat. 16: 85-122.
HOWE, H. (1981) Dispersal of a neotropical nutmeg (Virola sebifera) by birds. The Auk 98: 88-98.
HOWE, H.F. and G.F. ESTABROOK (1977) On intraspecific competition for avian dispersers in tropical trees. Amer. Nat. 111: 817-832.
ILLIGER, C. (1804/1811) Ueberblick der Säugethiere nach ihrer Vertheilung uber die Welttheile. Abd.K.pr.Akad.Wiss.
IZAWA, K. (1975) Foods and feeding behaviors of monkeys in the upper Amazon basin. Primates 16: 295-316.
IZAWA, K. (1976) Group sizes and compositions of monkeys in the upper Amazon basin. Primates 17: 367-399.
IZAWA, K. (1978) Frog-eating behavior of wild black-capped capuchin (Cebus apella). Primates 19: 633-642.

IZAWA, K. (1979) Foods and feeding behavior of the wild black-capped capuchin (Cebus apella). Primates 20: 57-76.

IZAWA, K. (1980) Social behavior of the wild black-capped capuchin (Cebus apella). Primates 21: 443-467.

JANSON, C.A. (in prep) Preliminary results of the effects of aggression and competition on the control of group size in the brown capuchin.

JANSON, C. and J.TERBORGH (in press) Censusing primates in rain-forest. Serie Zoologica, Museu de Historia Natural Javier Prado, Lima.

JANSON,C.H., J.TERBORGH and L.H.EMMONS (1981) Non-flying mammals as pollinating agents in the Amazonian forest. Reproductive Botany (Suppl. to Biotropica 13) : 1-6.

JOLLY, A. (1972) The evolution of primate behavior. MacMillan, New York.

KERR, R. (1792) The animal kingdom, a zoological system of the celebrated Sir Charles Linnaeus ..... Class I. Mammalia .... being a translation of that part of the Systema Naturae, as lately published ... by Prof.Gmelin .... with additions from more recent writers .... . Edinburgh.

KINZEY, W.K. (1980) Distribution of some Neotropical primates and the model of Pleistocene forest refugia. Fifth Int. Assoc. Trop. Biol. Symp., La Guaira, Venezuela.

KINZEY, W.G. (1981) The titi monkeys, Genus Callicebus. pp.241-276 IN Ecology and behavior of neotropical primates, Vol.1, A.F.Coimbra-Filho and R.A.Mittermeier EDS., Academia Brasileira de Ciências, Rio de Janeiro.

KINZEY, W.G. and M. BECKER (in press) Activity pattern of the masked titi monkey, Callicebus personatus. Primates.

KINZEY, W.G. and J.ROBINSON (1981) Intergroup loud calls serve different roles in two species of Callicebus. Am.J.phys.Anthrop. 54: 240.

KLEIN, L.L. and D.J.KLEIN (1973) Observations on two types of neotropical primate intertaxa associations. Am.J.phys.Anthrop. 38: 649-653.

KLEIN, L.L and D.J. KLEIN (1976) Neotropical primates: aspects of habitat usage, population density and regional distribution in La Macarena, Colombia. Pp 70-78 IN Neotropical primates: field studies and conservation, R.W. Thorington,Jr. and P.G.Heltne EDS., Nat.Acad.Sci.

KLEIN, R.M. (1975) Southern Brazilian phytogeographic features and the probable influence of upper quaternary climatic changes in the floristic distribution. Boletim Paranaense de Geociências 33: 67-88.

KUHL, H. (1820) Beiträge zur zoologie und vergleichenden anatomie. Part 1. Verlag der Hermannschen Buchhandlung, Frankfurt.

KUHLHORN, F. (1939) Beobachtungen uber das Verhalten von Kapuziner-affen in freier Wildbahn. Zeitch. fur Tierpsychologie 3: 147-151.

KUHLHORN, F. (1943a) Beobachtungen uber die biologie von Cebus apella. D.Zool.Garten 15: 221-234 [apud Hill 1960].

KUHLHORN, F. (1943b) Tier und Umwelt in Sudamerika. Hamburg, Ibero- Amerik.Int. [apud Hill 1960].

KUHLHORN, F. (1953) Natur.u.Volk, 83: 115-119 [apud Hill 1960].

KUHLHORN, F. (1955) Saugetierk.Mitt. 3: 156-164 [apud Hill 1960].

KUHLMANN, M. (1975) Adenda alimentar dos bugios. Silvic.S.Paulo 9:

57-62.
LACHER Jr., T.E, G.A.B.FONSECA, C.ALVES JR. and B.MAGALHÃES-CASTRO (1981) Exudate-eating, scent-marking and territoriality in wild populations of marmosets. Animal Behaviour 29 (1): 306-307.
LAEMMERT, H.W.Jr, L.CASTRO FERREIRA and R.M.TAYLOR (1946) An epidemiological study of jungle yellow fever in an endemic area in Brazil. Part II. Investigations of vertebrate hosts and arthropod vectors. American J.Trop. Med. 26(6): 23-60.
LIMA, E.C. (1945) Mammals of Amazonia (Vol.I) Museu Paraense Emílio Goeldi de Historia Natural e Etnografia. Belém and Rio de Janeiro.
LINNAEUS, C. (1758) Systema naturae, Tomus I, 10th edition.
LINNAEUS, C. (1766) Systema naturae, Tomus I, 12th edition.
LONNBERG, E. (1939) Remarks on some members of the genus Cebus. Arkiv. for zoologi. Bd 31A n.23: 1-24.
MAIER,W., C.ALONSO and A.LANGGUTH (1982) Field observations on Callithrix jacchus jacchus L.. Zeitschrift fur Saugetierkunde 47 (6): 334-345.
MARRIOTT, F.H.C. (1974) The interpretation of multiple observations. Academic Press, London, New York & S.Francisco.
MASON, W.A. (1968) Use of space by Callicebus groups. IN Primates Studies in Adaptation and Variability. ED. P.C.Jay. Holt, New York.
MILTON, K. (1980A) Efficiency vs. velocity: digestive strategies of two primate species. Abstracts of the VIII Intern.Congr. of Primatology 3(2): 241.
MILTON, K. (1980B) The foraging strategy of howler monkeys - a study in primate economics. Columbia University Press, New York, 165 pp.
MIRANDA RIBEIRO, A. (1924) Alguns factos e mais dois símios novos da nossa fauna. Boletim do Museu Nacional do Rio de Janeiro I (3): 211-215.
MITTERMEIER, R. (1977) Distribution, synecology and conservation of Surinam monkeys. Unpublished doctoral dissertation, Harvard University, Cambridge.
MITTERMEIER, R. and A.F. COIMBRA-FILHO (1981) Systematics: species and subspecies. pp.29-109 IN Ecology and behavior of neotropical primates, Vol.1, EDS. Coimbra-Filho, A. and R.Mittermeier. Academia Brasileira de Ciências, Rio de Janeiro.
MITTERMEIER, R. and M. ROOSMALEN (1981) Preliminary observations on habitat utilization and diet in eight Surinam monkeys. Folia primat. 36: 1-39.
MONTEIRO, C.A.F. (1976) O clima e a organização do espaço no Estado de São Paulo: problemas e perspectivas. Série Teses e Monografias 28, Instituto de Geografia da Universidade de São Paulo, São Paulo.
MORI,S.A., G.T.PRANCE and A.B.BOLTEN (1978) Additional notes on the floral biology of neotropical Lecythidaceae. Brittonia 30 (2): 113-130.
MOYNIHAN, M. (1976) The New World primates. Princeton University Press, Princeton, New Jersey.
MULLER, P. (1973) The dispersal centres of terrestrial vertebrates in the neotropical realm. Biogeographica II, W.Junk B.V.Publishers, The Hague.
NAPIER, P.H. (1976) Catalogue of primates in the British Museum

(Natural History) Part I: families Callitrichidae and Cebidae. British Museum (Natural History), London.
NAPIER,J. and P.H. NAPIER (1967) A handbook of living primates. Academic Press, London and New York.
NELLIS, C.H., S.P.WETMORE and L.B.KEITH (1978) Age-related characteristics of coyote canines. J.Wildl.Manage. 42 (3): 680-683.
NIE, N.H., C.H.HULL, J.G.JENKINS, K.STEINBRENNER and D.H.BENT (1975) S.P.S.S.- Statistical Package for the Social Sciences, 2nd.edition, McGrawHill, New York.
NIMER, E. (1977) Clima. pp 51-89 IN Geografia do Brasil (Vol.3 - Região Sudeste) Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.
NISHIMURA, A. (1979) In search of woolly spider monkey. pp.21-37 IN Kyoto Univ.Overseas Research Reports on New World Monkeys 1979. Kyoto Univ. Primate Research Institute.
OPPENHEIMER, J.R. (1968) Behavior and ecology of the white faced monkey Cebus capucinus on Barro Colorado Island. Unpublished PhD thesis, University of Illinois, Urbana.
OPPENHEIMER, J.R. (1969a) Changes in forehead patterns and group composition of the white-faced monkey. pp.36-42 IN Proc.2nd.int.Congr.Primat., Atlanta, GA, 1968. Vol.1, Karger, Basel/New York.
OPPENHEIMER, J.R. (1969b) Cebus monkeys: effect on branching of Gustavia trees. Science 165: 187-188.
OPPENHEIMER, J.R. (1969c) Cebus capucinus: play and allogrooming in a monkey group. American Zoologist 9 (4).
OPPENHEIMER, J.R. (1977) Forest structure and its relation to activity of the capuchin monkey (Cebus). pp.74-84 IN Use of non human primates in biomedical research. EDS. M.R.N.Prasad and T.C.A.Kumar. Indian National Science Academy, New Delhi.
OREN, D. (1979) Testing the refugium model for South America: a hypothesis to evaluate discrepancies in refugia number across taxa. Manuscript for a conference delivered at the Fifth Int.Symp. Assoc. Trop. Biol., Caracas.
OYEN, O.J. and D.H.ENLOW (1981) Structural-functional relationships between masticatory skeletal biology and craniofacial development in primates. pp. 93-97 IN Evolutionary Biology. Selected papers (Part A) of the VIII Congress of the Intern.Primatological Soc., Florence, July 1980. EDS. A.B.Chiarelli and R.S.Corruccini. Springer-Verlag, Berlin/New York.
PINTO, O. (1941) Da validez de Cebus robustus Kuhl e de suas relações com as formas mais afins. Papéis avulsos do Departamento de Zoologia 1: 111-120.
PINTO, O. (1945) Cinqüenta anos de investigação ornitológica. Arq.de Zool. do Estado de S.Paulo 4: 261-340.
PIRES, F.D.A. (1965) The type specimens of Brazilian mammals collected by Prince Maximilian zu Wied. Amer.Mus.Novit. 2209.
PRANCE, G. (1974) Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalacae and Lecythidaceae. Acta Amazonica 3 (3): 5-28.
PRANCE, G.T. (1980) A note on the probable pollination of Combretum by Cebus monkeys. Biotropica 12 (3): 239.

PUCHERAN, J. (1857) Notices mammalogiques C.Genre Cebus. Rev.et Mag. de Zoologie, 2e.serie, T.IX, pp.337-352.
PUSCH, B. (1941) Die Arten der Gattung Cebus. Z.Saugetierk 16: 183-237.
QUINE, D.B. (1981) Fluctuations in outdoor sound propagation: implications for animal communication. Abstracts of the XVII International Ethological Conference, 1-9 September, Oxford.
QURIS, R. (1980) Emission vocale de forte intensité chez Cercocebus galeritus agilis: structure, caractéristiques spécifiques et individuelles, modes d'émission. Mammalia, 44 (1): 35-50.
RAFFAUF, R.F. (1970) A handbook of alkaloids and alkaloid-containing plants. Wiley-Interscience, New York.
RAINIER, P. and G.H.BOURNE EDS. (1977) Primate conservation. Academic Press, New York.
RANZANI, G. and J.E. PESSOTTI (1975) Carta de solos da Fazenda Barreiro Rico - Cia.Itaquerê Industrial e Agrícola (1:25.000 , 15289 ha).
RATTER, J.A. (1980) Notes on the vegetation of fazenda Água Limpa (Brasília, DF, Brazil). Royal Botanic Garden, Edinburgh, 111pp.
RED DATA BOOK (1982) The I.U.C.N. Mammal Red Data Book (compiled by J.Thornback and M.Jenkins). I.U.C.N.
REMINGTON, C.L. (1968) Suture-zones of hybrid interaction between recently joined biotas. Evolutionary biology 2.
RENGGER, J.R. (1830) Naturgeschichte der Saeügenthiere von Paraguay. Schweighauserchen Buchlandlung, Basel.
RIZZINI, C.T. and A.F. COIMBRA-FILHO (1981) Lesões produzidas pelo sagüi Callithrix p.penicillata (E.Geoffroy, 1812) em árvores do cerado. Rev.Brasil.Biol. 41 (3): 579-583.
ROBINSON, J.G. (1979) Correlates of urine washing in the wedge capped capuchin Cebus nigrivittatus. IN Vertebrate Ecology in the Northern Neotropics, J.F.Eisenberg ED., Smithsonian Institution Press, Washington, D.C.
ROBINSON, J. (1981) Spatial structure in foraging groups of wedge-capped capuchin monkeys Cebus nigrivittatus. Anim.Behav. 29: 1036-1056.
RODE, P. (1938) Catalogue des types de mammifères du Muséum National d'Histoire Naturelle. I. Ordre des Primates. A.Sous-ordre des Simiens. Muséum National d'Histoire Naturelle, Paris.
ROMER,A.S. and T.S.PARSONS (1977) The vertebrate body. W.B.Saunders, Philadelphia.
RUSCHI, A. (1964) Macacos do Estado do Espírito Santo. Boletim do Museu de Biologia Prof.Mello Leitão 23-A: 1-23.
RYLANDS, A.B. (1979) Preliminary observations on the marmoset Callithrix humeralifer intermedius (Hershkovitz 1977) at Dardanelos, R.Aripuanã, Mato Grosso. Acta Amazonica 9 (3): 2-33.
RYLANDS, A.B. (1982) Ecology and behaviour of three species of Callitrichidae. PhD thesis, University of Cambridge.
SÃO PAULO (1972) Atlas pluviométrico do Estado de São Paulo (período 1941 a 1970). Departamento de Águas e Energia Elétrica, Centro Tecnológico de Hidráulica, São Paulo.
SETZER, J. (1942) Os solos dos grupos n.11 a 14. Bol.Agric.(1942): 268-312. São Paulo.
SETZER,J. (1966) Atlas climático e ecológico do Estado de São

Paulo. Comissão Interestadual da Bacia do Paraná. Centrais Elétricas de São Paulo, São Paulo.

SILVA, E.C. (1981) A preliminary survey of brown howler monkeys (Alouatta fusca) at the Cantareira Reserve (São Paulo, Brazil). Rev.Brasil.Biol. 41 (4): 897-909.

SIMPSON, B.B. and J. HAFFER (1978) Speciation patterns in the Amazonian forest biota. Ann.Rev.Ecol.Syst. 9: 497-518.

SNOW, D. (1962) The natural history of the oilbird Steatornis caripensis, in Trinidad, W.I. Part 2. Population, breeding, ecology and food. Zoologica 46 (3): 27-48.

SNOW, D. (1981) Tropical frugivorous birds and their food plants: a world survey. Biotropica 13(1): 1-14.

SOKAL, R.R. and R.C. RINKEL (1963) Geographic variation of alate Pemphigus populi-transversus in Eastern North America. Univ.Kansas Sci.Bull. 44 (10): 467-507.

SPIX, J. (1823) Simiarum et Vespertilionum Brasiliensium Species Novae. F.S.Hubschmann, Monaco.

STEVENSON, M. (1978) The behaviour and ecology of the common marmoset (Callithrix jacchus jacchus) in its natural environment. P.298 IN Biology and behaviour of marmosets. EDS. H.Rothe, H.J.Wolters and J.P.Hearn. (Proceedings of the Marmoset Workshop, Gottingen, W.Germany, September 2-5, 1977), Eigenverlag Rothe, Gottingen.

STEVENSON, M.F. and A.B.RYLANDS (in press) The marmoset monkeys, genus Callithrix. IN Ecology and Behaviour of Neotropical Primates, Vol.2, EDS. A.F.Coimbra-Filho and R.Mittermeier. Academia Brasileira de Ciências, Rio de Janeiro.

STRUHSAKER, T.T. and L.LELAND (1977) Palm-nut smashing by Cebus apella apella in Colombia. Biotropica 9 (2): 124-126.

TATE, G.H.H. (1954) On Cebus apella (Linnaeus) with a note on Cebus capucinus (Linnaeus). J.Mamm. 35:415-418.

TEIXEIRA,J.P.F., H.A.A.MASCARENHAS and O.C.BATAGLIA (1979) Efeito de cultivares, tipos de solo e práticas culturais sobre a composição química de sementes de soja (Glycine max (L) Merrill). Anais do I Semin. Nac. de Pesq. de Soja I: 11-16.

THOMAS, O. (1901) New mammals from Peru and Bolivia, with a list of those recorded from the Inambari River, upper Madre de Dios. Ann.Mag.Nat.Hist. 7 (7): 178-190.

THORINGTON, R.W. (1967) Feeding and activity of Cebus and Saimiri in a Colombian forest. IN Progress in Primatology. EDS. D.Starck, R.Schneider and H.J.Kuhn. Gustav Fischer Verlag.

THORINGTON, R.W. (1968) Observation of squirrel monkeys in a Colombian forest pp.69-85 IN The Squirrel Monkey. EDS. L.A.Rosemblum and R.W.Cooper. Academic Press, New York.

THORINGTON, R.W.(1976) The systematics of New World monkeys. pp.8-18 IN First Inter-American Conference on conservation and utilization of American non-human primates in biomedical research, Pan American Health Organisation, Washington, D.C.

THORINGTON, R.W. (1978) Some problems relevant to the conservation of the Callitrichidae. Prim. Med. 10: 1-11 (EDS. E.Goldsmith and J.Moor-Jankowski, S.Karger, Basel).

THORINGTON, R.W. and P.G.HELTNE EDS. (1976) Neotropical primates - field studies and conservation. (Proceedings of a symposium on the distribution and abundance of neotropical primates) National Academy of Sciences, U.S.A.

THORINGTON, R.W., D.RUDRAN and D.MACK (1979) Sexual dimorphism of

Alouatta seniculus and observations on capture techniques. IN Vertebrate Ecology in the Northern Neotropics. J.Eisenberg ED. Smithsonian Institution Press, Washington D.C.

THORPE, R.S. (1976) Biometric analysis of geographic variation and racial affinities. Biol.Rev. 51: 407-452.

TORRES DE ASSUMPÇÃO, C. (1981) Cebus apella and Brachyteles arachnoides (Cebidae) as potential pollinators of Mabea fistulifera (Euphorbiaceae). J.Mamm. 62 (2): 386-388.

TORRES DE ASSUMPÇÃO, C. (1983) Conservation of primates in Brazil: Atlantic forest primates. Pp. 34-48 IN Proceedings of the Symposium on the Conservation of Primates and their habitats, (24-25 September 1982 Leicester), Vol.I, Vaughan Paper N.31, Univ. Leicester.

TORRES DE ASSUMPÇÃO, C. (in press) Ecological and behavioural information on Brachyteles arachnoides. Primates.

TORRES DE ASSUMPÇÃO, C. and J.M.DEAG (1979) Attention structure in monkeys: a search for a common trend. Folia primatol. 31: 285-300.

TORRES DE ASSUMPÇÃO, C., H. LEITÃO FILHO and O. CESAR (1982) Descrição das matas da fazenda Barreiro Rico, Estado de São Paulo. Revta.brasil.Bot. 5 (1-2): 53-66.

TORRES DE CABALLERO,O.H., C.RAMIREZ and E.YUNISK (1976) Genus Cebus Q- and G-band karyotypes and natural hybrids. Folia primatol. 26: 310-321.

VAN DER PIJL, L. (1969) Principles of dispersal in higher plants. Springer-Verlag, Berlin.

VAN DER HAMMEN, T. (1974) The Pleistocene changes of vegetation and climate in tropical South America. Journal of Biogeography 1, Curitiba.

VANZOLINI, P.E. (1967) Problems and programs in Amazonian zoology. Atas do Simpósio sobre a Biota Amazonica 5: 85-95.

VANZOLINI, P.E. (1970) Zoologia sistemática, geografia e a origem das espécies. Série Teses e Monografias 3, Instituto de Geografia da Universidade de São Paulo, São Paulo.

VANZOLINI, P.E. (1973) Paleoclimates, relief and species multiplication in equatorial forests. IN Tropical forest ecosystems in Africa and South America: a comparative review, B.J.Meggers, E.S.Ayensu and W.D.Duckworth EDS., Smithsonian Institution Press, Washington D.C.

VANZOLINI, P.E. and N. PAPAVERO (1968) Índice de topônimos contidos na carta do Brasil 1:1.000.000 do I.B.G.E. Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), São Paulo.

VANZOLINI, P.E. and E.E. WILLIAMS (1970) South American anoles: the geographic differentiation and evolution of the Anolis chrysolepis species group (Sauria, Iguanidae). Arq.Zool, S.Paulo, 19 (1-2): 1-124.

VAURIE (1972) An ornithological gazetteer of Peru. Amer.Mus.Novit. 2491.

VICTOR,M.A.M. (1975) A devastação florestal. Sociedade Brasileira de Silvicultura, São Paulo.

VIEIRA, C. (1944) Os símios do Estado de São Paulo. Pap.Avuls.S.Paulo 4 (1): 1-31.

VIEIRA, C. (1955) Lista remissiva dos mamíferos do Brasil. Arquivos Zoologia S.Paulo 8: 341-474.

WALTER, H. and H. LEITH (1967) Klimadiagramm-Weltatlas VEB Gustav

Fischer Verlag, Jena [apud Eisenberg et al. 1981] .
WASER, P.M. (1982) Primate polyspecific associations: do they occur by chance? Anim. Behav. 30:1-8.
WIED-NEUWIED, M. (1820) Travels in Brazil in the years 1815, 1816, 1817. Part 1. Henry Colburn and Co., London.
WIED-NEUWIED, M. (1826) Beiträge zur naturgeschichte von Brasilien. II.Band. Weimar, Verlage.
WILLIS, E.O. (1979) The composition of avian communities in remanescent woodlots in southern Brazil. Papéis Avulsos Zool., São Paulo, 33 (1):1-25.
WISHARD, D. (1982) CLUSTAN - Cluster Analysis Package. 3rd edition. Inter-University/Research Council Series - Report n.47. Program Library Unit, Edinburgh University.
ZUCKERMANN,S. (1933) Functional affinities of man, monkeys and apes. Kegan, Paul, Trench, Trubner & Co, London.

APPENDICES

APPENDIX I.1
PLANT SPECIES SAMPLED AT BARREIRO RICO

The field number is given for the samples which have not been identified to species level.
Specimens from most species were deposited at the herbarium of the Universidade Estadual de Campinas, and a whole collection was kept for use of field workers at the site.
Legend:
t - trees; s - shrubs; l - lianas; h - herbs; e - epiphytes
fsp - forest species
osp - open formation species

ACANTHACEAE
- Ruellia sp. (h,fsp)
- Mendoncia coccinea Vell. (l)

ANACARDIACEAE
- Astronium graveolens Jacq. (guaritá) (t,fsp)

APOCYNACEAE
- Aspidosperma nemorale Handro (guatambú) (t,fsp)
- Aspidosperma peroba Saldanha da Gama (peroba) (t,fsp)
- Condylocarpum sp. (l)
- Mandevilla sp. (l)
- Peschiera fuchsiaefolia (.dc.)Miers (leiteira da invernada)(s)

ANNONACEAE
- Annona cacans Warm. (araticum) (t,fsp)
- Duguetia furfuracea (.st. Hil.)Benth.& Hook. (pinha do cerrado)(s,osp)
- Duguetia lanceolata St. Hil. (pindaíba) (t,fsp)
- Guatteria sp. (l)
- Xylopia brasiliensis Spreng. (erva-doce) (t,fsp)

AQUIFOLIACEAE
- Ilex cerasifolia Lam. (t,fsp)

ARACEAE
- Philodendron sp. (imbê) (e,fsp)

ARALIACEAE
- Didymopanax morototoni Decne. & Planch. (mandioqueiro) (t,fsp)
- Didymopanax vinosum (Cham. & Sch.) Marck. (s,osp)

BIGNONIACEAE
- Adenocalymma sp. (l)
- Anemopaegma sp. (l)
- Arrabidaea sp. (l)
- Callychlamys sp. (l)
- Fridericia speciosa Mart. (l)
- Lundia sp. (l)
- Melloa quadrivalvis (Jacq.) A.Gentry (l)
- Pithecoctenium sp. (pente de macaco) (l)
- Pyrostegia venusta Miers (flor de s.João) (l)
- Stizophyllum perforatum Miers (l)
- Tabebuia vellosoi Toledo (am. 7555) (ipê) (t,fsp)
- Zeyhera tuberculosa (Vell.) Bur. (bolsa de pastor) (t,fsp)

BORAGINACEAE
- Cordia ecalyculata Vell. (café de bugre) (t,fsp)
- Cordia sellowiana Cham. (açuquinha da mata) (t,fsp)

CARICACEAE
- Jacaratia spinosa (Aublet) A. DC. (jaracatiá) (t,fsp)

CELASTRACEAE
Maytenus sp. (am. 7571, 7589) (t,fsp)
COMPOSITAE
Baccharis dracunculifolia DC. (alecrim do campo) (s,osp)
Calea clausseniana Baker (h,osp)
Gochnatia pulchra Cabr. (s,osp)
Piptocarpha macropoda (DC.) Baker
Vernonia cognata Less. (h,osp)
Vernonia scorpioides (Lam.) Pers. (h,osp)
CUNONIACEAE
Lamanonia glabra Camb. (t,fsp)
CYPERACEAE
Rhynchospora exaltata Kunth. (navalha de macaco) (h)
DICLIDANTHERACEAE
Diclidanthera sp (cipó jabuticaba) (l)
DIOSCOREACEAE
Dioscorea sp. (l)
ELAEOCARPACEAE
Sloanea monosperma Vell. (bugreiro, ouriço) (t,fsp)
ERYTHROXYLACEAE
Erythroxylum campestre St. Hil. (t,osp)
Erythroxylum pelleterianum St. Hil. (s,osp)
EUPHORBIACEAE
Actinostemon estrellensis (Muell. Arg.) Pax (pau de espeto) (s,fsp)
Alchornea triplinervia Muell.Arg. (tapiazeiro) (t,fsp)
Aparisthmium cordatum Baill. (boleiro) (t,fsp)
Croton floribundus Spreng. (capexingui) (t,fsp)
Gonatogyne brasiliensis Muell. Arg. (guaraiúva branca) (t,fsp)
Mabea fistulifera Mart.(canudeira-de-pito, leiteira-do-mato) (t,fsp)
Pachystroma illicifolium (Klotzch.) Muell.Arg. (canxim) (t,fsp)
Pera obovata Baill. (t,fsp)
Sebastiania sp.1 (am. s/n) (h,osp)
Sebastiania sp.2 (am. s/n) (t,fsp)
Securinega guaraiuva Kuhlm. (guaraiúva) (t,fsp)
FLACOURTIACEAE
Casearia inaequilatera Camb. (guassatonga) (t,fsp)
GRAMINEAE
Merostachys sp. (taquari) (fsp)
Ichnanthus sp. (h,fsp)
GUTTIFERAE
Rheedia gardneriana Planch. & Triana (t,fsp)
ICACINACEAE
Villaresia sp. (am. 7569) (t,fsp)
LAURACEAE
Cryptocarya moschata Nees et Mart. (batalheira, canela-batalha) (t,fsp)
Nectandra sp. (canela cheirosa) (t,fsp)
Ocotea acutifolia (Nees.) Mez. (canela preta) (t,fsp)
Ocotea aff. spixiana (Nees.) Mez. (canelão) (am. 7528) (t,fsp)
Ocotea pulchella Mart. (s,osp)
LECYTHIDACEAE
Cariniana estrellensis (Raddi) O. Kuntze (jequitibá) (t,fsp)
LEGUMINOSAE
Acacia plumosa Lowe (cipó de espinho) (l)
Acacia polyphylla DC. (monjoleiro, gorocaia) (t,fsp)
Bauhinia sp. (l)
Cassia aff. rugosa (s,osp)

Copaifera langsdorfii Desf. (pau de óleo) (t,fsp & osp)
Dalbergia variabilis Vog. (l)
Dioclea sp. (cipó coronha) (l)
Hymenaea courbaril L. (jatobá) (t,fsp)
Inga striata Benth. (inga) (t,fsp)
Stryphnodendron adstringens (Mart.) Colville (barbatimão) (t,osp)
Zollernia ilicifolia Vog. (pau jantar) (t,fsp)

LOGANIACEAE
Strychnos brasiliensis Mart. (salta martí) (s)
Strychnos sp. (h,osp)

LORANTACEAE
(not identified) (am. 7536) (e)

MAGNOLIACEAE
Talauma ovata St. Hil. (pinha do brejo) (t,fsp)

MALPIGHIACEAE
Byrsonima intermedia A. Juss. (s,ops)
Heteropteris sp. (l)
(not identified) (am. s/n) (l)

MELASTOMATACEAE
Miconia albicans (Sw.) Triana (s)
Miconia candolleana Triana (s,fsp)
Miconia fallax DC. (s)
Miconia langsdorfii Logn. (h)
Miconia sp. (am. 7552) (t,fsp)
Mouriri sp. (am. 7521) (pitanga brava) (t,fsp)
(not identified) (am. 7553) (s)
(not identified) (am. 7560) (h)

MONIMIACEAE
Siparuna sp. (limão bravo do mato) (am.7522) (s,fsp)

MORACEAE
Cecropia hololeuca Miq. (embaúba) (t,fsp)
Ficus sp. (figueira) (e)

MYRSINACEAE
Rapanea guyanensis Aublet (am. 7545) (carne de vaca) (t,fsp)
Rapanea lancifolia (Mart.) Mez (s,osp)

MYRTACEAE
Blepharocalyx sp. (s,osp)
Callyptrogenia sp. (am. 7563) (piúna) (t,fsp)
? Campomanesia (am. 7578) (s,osp)
Eugenia pyriformis Camb. (uvaia) (t,fsp)
Eugenia sp. (am. 7517) (t,fsp)
Eugenia squamulosa Mattos (s,fsp)
Gomidesia sp.1 (am. 7524) (brasa viva) (t,fsp)
Gomidesia sp.2 (am. 7530) (t,fsp)
Myrcia obtecta (Berg.) Kiaersk. (s)
Myrcia formosiana DC. (am. 7520) (t,fsp)
Myrcia sp.1 (am. 7574) (s,osp)
Myrcia sp.2 (am. 7576) (s,osp)
Myrcia sp.3 (am. s/n) (s,osp)
Myrciaria sp. (am. 7532) (cambuí) (t,fsp)
Myrceugenia sp. (am s/n) (t,osp)
Psidium sp. (am. 7546, 7559) (t,fsp)

OCHNACEAE
Ouratea salicifolia Engl. (t,fsp)

OPILIACEAE
Agonandra brasiliensis Miers (t,fsp)

PALMAE
Syagrus campestris (Mart.) Wendl. (h,osp)
Syagrus sp. (am. s/n) (coqueiro) (t,fsp)
PHYTHOLACACEAE
Seguieria langsdorfii Mog. (l)
PIPERACEAE
Ottonia sp. (am. 7564) (s,fsp)
Peperomia sp. (e,fsp)
Piper sp. (am. 7585) (s,fsp)
POLYGONACEAE
Coccoloba sp. (am. 7579) (taxi, taxizeiro) (t,fsp)
PROTEACEAE
Roupala sp. (am. s/n) (t,fsp)
RHAMNACEAE
Rhamnidium elaeocarpum Reiss. (saguaragi amarelo) (t,fsp)
RUBIACEAE
Alibertia sp. (am. 7519) (s,fsp)
Amaioua guianensis Aublet (t,fsp)
Chiococca brachiata Ruiz & Pav. (l)
Faramea sp. (am. 7544) (s,fsp)
Palicourea rigida H. B. K. (h)
Palicourea sp. (h,fsp)
Psychotria vauthieri Muell. Arg. (am. 7558) (t,fsp)
Psychotria sp.1 (am. 7565) (t,fsp)
Psychotria sp.2 (am. s/n) (h,fsp)
Psychotria sp.3 (am. 7535,7582) (pipoca) (h,fsp)
Tocoyena formosa (Cham. & Sch.) K. Sch. (s,osp)
RUTACEAE
Esenbeckia febrifuga A. Juss (mamoninho) (s,fsp)
Esenbeckia intermedia Mart. (canela de cotia) (t,fsp)
Esenbeckia leiocarpa Engl. (guarantã) (t,fsp)
Galipea jasminiflora Engl. (mamoninha) (t,fsp)
Metrodorea nigra St. Hil. (carrapateira) (t,fsp)
Pilocarpus pauciflorus St. Hil. (amendoím torrado) (t,fsp)
Zanthoxylum rhoifolium Lam. (mamica de porca) (t,fsp)
SAPINDACEAE
Cupania sp. (am. 7557) (arco de peneira) (s,fsp)
Paullinia sp. (l)
Serjania sp. (l)
SAPOTACEAE
Chrysophyllum gonocarpum (Mart. et Eichl.) Engl. (t,fsp)
SOLANACEAE
Solanum megalochiton Mart. (s,fsp)
Solanum sp.1 (am. 7587) (s,fsp)
Solanum sp.2 (am. s/n) (jurubeba) (s,fsp)
Solanum swartzianum (folha de prata) (s,fsp)
STERCULIACEAE
Guazuma ulmifolia Lam. (coração de negro) (t,fsp)
TILIACEAE
Prockia crucis L. (t,fsp)
ULMACEAE
Celtis spinosa Spreng. (galinha choca) (t,fsp)
VERBENACEAE
Aegiphila sp. (s)
Lippia sp. (h)
VIOLACEAE

Hybanthus atropurpureus Taub. (h)

VOCHYSIACEAE

Vochysia tucanorum Mart. (cinzeiro) (t,fsp)

Qualea jundiahy Warm. (pau terra, goiaba do mato) (t,fsp)

APPENDIX I.2
FOOD ITEMS OF B.R. PRIMATES

DESCRIPTION OF FOOD ITEM	APPROXIMATE PERIOD WHEN ITEM WAS AVAILABLE (o)	ITEM UTILIZED BY: (o)				
		CEBUS (obs. 285 h)	ALOUATTA (obs. 41 h)	BRACHYTELES (obs. 23 h)	CALLICEBUS (obs. 4 h)	CALLITHRIX (obs. 12 h)
1.CRYPTOCARYA MOSCHATA - Ripening fruit. Mature seeds not seen to be ingested; Brachyteles may ingest immature ones Positive for alkaloids.	** XII to III	S I(3) II(1) III(10) P=3.5	I(3) II(2) P=1.25	S XII(4) I(1) II(3) III(3) P=2.75	III(1) P=0.25	
2.EUGENIA SP(sample 7517) - Ripe (orange) fruit. Mature seeds are ingested with the fruit flesh. Negative for alkaloids	** II & III	S II(1) III(2) P=1.5		II(4) P=2.0		
3.ESENBECKIA LEIOCARPA - Forming seeds; eaten only at early stages of seed formation. Negative for alkaloids	** from II to. VI, differ. stages of maturation	D III(4) P=?		D II(1) P=?		
4.COPAIFERA LANGSDORFII - Ripe/ripening aril. Fruits are forced open by Cebus. Negative for alkaloids	** VI to VIII	VI(11) VII(10) VIII(6) P=9.0		S VI(3) (VII?) VIII(1) P=1.3		
5.PSYCHOTRIA SP (sample 7565) - Ripe fruit Negative for alkaloids	** XII to II	S I(2) P=0.66				
6.MABEA FISTULIFERA - Nectar Not tested for alkaloids	I to VI	II(1) III(12) IV(16) V(21) P=8.3		IV(2) P=0.33		
7. - Immature/mature seeds Cebus removes seeds before fruit dehiscence Negative for alkaloids.	** VI to X	D VII(2) VIII(11) IX(16) X(4) P=6.6				

8. - Leaves Not tested for alkaloids	no notes		VIII(1)? P=?			
9.FARAMEA SP(sample 7544) - Ripe (violet) fruit Not tested for alkaloids	(peak) XII & I	S I(2) P=1.0				
10.OCOTEA AFF.SPIXIANA - Ripening fruit Negative for alkaloids	** VIII to XI	S IX(3) X(1) P=1.0				
11. - Shoots and/or very young fruit Not tested for alkaloids	no notes			VIII(1) P=?		
12.PHILODENDRON SP. - Immature female flowers Cebus rips the bracts to get the flowers Negative for alkaloids	** no notes	XI(1) XII(2) I(1) P=?				
13. - Mature leaves The largest veins are avoided. Negative for alkaloids	** year round		I(3) P=0.25			
14.MICONIA CANDOLLEANA - Ripening/ripe (dark blue) fruit.	(peak) IV to VI	S VIII(2) P=0.66				
15.MOURIRI SP. - Immature seeds Negative for alkaloids	** II to VIII at least	D II(1) VI(2) P=?				
16. - Seed-coating mucilage. Seeds are also ingested. Not tested for alkaloids	IX and X	S IX(1) X(2) P=0.5				
17. - Shoots Not tested for alkaloids	no notes			XIII(1) P=?		
18.MICONIA SP(sample 7552) - Ripe (blackish-violet) fruit. Negative for alkaloids	** VII & VIII	S VIII(1) P=0.5				
19.XYLOPIA BRASILIENSIS - Maturing/mature seeds Cebus may force the fruit	** IX & X	D IX(2)				

open to get the seeds. Negative for alkaloids		X(2) P=2.0					
20.QUALEA JUNDIAHY - Forming (very tender) seeds. The thick outer layer of fruit is discarded. Negative for alkaloids	** fruit: I to VIII, (varying ripeness)	D V(2) P=?					
21. - Shoots Not tested for alkaloids	no notes				XII(1) P=?		
22.DUGUETIA LANCEOLATA - Immature fruit (only whitish matter around forming seeds) Positive for alkaloids	** XII to II	D XII(1) I(1) II(1) P=1.0					
23. - Ripe/ripening fruit (pink watery matter around seeds)	XII to II				S XII(2) (I),II(2) P=1.3		
24.ASPIDOSPERMA PEROBA - Forming fruit (less than 5 cm long) Negative for alkaloids	** at least XII and I		D I(8) I(1) P=3.0				
25.ASTRONIUM GRAVEOLENS - Gum Negative for alkaloids	** year round?					IX(3) X(6) P=?	
26. - Petioles Not tested for alkaloids	no notes		X(1) P=?				
27.ZEA MAYS - Grain (i.e., fruit) Cebus seem to eat only part of the grain, including the germ	** -during crops -bait corn (used by hunters)	D I(1) II(1) III(1) VI(2) VII(7) IX(1)					
28.VILLARESIA SP - Maturing seeds (pericarp discarded) Not tested for alkaloids	IX & X	D IX(3) P=1.5					
29.GONATOGYNE BRASILIENSIS - Mature seeds (fruits are forced open) Negative for alkaloids	** XII to III	D,S XII(1) II(1) P=0.5					

30. - Immature leaves Not tested for alkaloids	no notes			VI(2) P=?		
31.HYPPOCRATEA SP - Maturing seeds (Fruit are forced open while still green) Not tested for alkaloids	no notes	D VI(1) VII(1) P=?				
32.INGA STRIATA - White (freshly open) flowers (only the basal part of the flower is eaten (for nectar?) Negative for alkaloids	** VIII to X	IX(6) P=2.0				
33. - Seeds & surrounding mucilage. (Fruit are forced open before dehiscence) Not tested for alkaloids	XII to III	XII(1) I(1) II(1) III(1) P=1.0	I? indic. from remains			
34. - Flower buds (closed) Not tested for alkaloids	VIII & IX		IX(2) P=1.0			
35.MYRCIA FORMOSIANA - Ripening/ripe fruit Seeds are ingested together with fruit flesh Negative for alkaloids	** XII to II	S I(1) II(1) III(1) P=1.0				
36. unidentified tree (ASTRONIUM GRAVEOLENS?) - Adult leaves Not tested for alkaloids	no notes		VII(1) P=?			
37. unidentified lianas (probably Bignoniaceae) - Adult leaves (veins are often avoided) Not tested for alkaloids	no notes		IX(2) XII(1,1) I(2,1,2,3,1) P=?	II(1)		
38. unidentified liana - Flower buds (clusters) Not tested for alkaloids	no notes		XI(1) P=?			
39. unidentified liana (with tendrils) - Young leaves Not tested for alkaloids	no notes		XII(1) P=?			
40. unidentified liana						

- Young leaves Not tested for alkaloids	no notes			XII(1)			
41.DICLIDANTHERA SP - Mucillage around seeds (seeds probably ingested) Not tested for alkaloids	X to XII	XII(4) P=1.3	XII (obs.by A.Nishi- mura)				
42.MENDONCIA COCCINEA - Mature fruit. Seeds are probably ingested Not tested for alkaloids	II & III	II(1) P=0.5					
43.(probably)ADENOCALYMMA - Flower buds (clusters) Not tested for alkaloids	no notes		I(2) P=?				
44. - Seeds (fruit are forced open before dehiscence) Not tested for alkaloids	no notes	D,S III(2) V(1) P=?					
45. Bignoniaceae (liana) - Terminal leaves Not tested for alkaloids	no notes		I(1) P=?				
46.HYMENAEA COURBARIL - Young leaves Not tested for alkaloids	VII & VIII			VIII(2) P=1.0			
47. - Powder around seeds Not tested for alkaloids	VII & VIII			~VIII (obs.by J.C.Ma- galhaes)			
48. - Immature seeds? Not tested for alkaloids	IV to VI	V (broken green pods)					
49.EUGENIA PYRIFORMIS - Mature seed (pericarp discarded) Negative for alkaloids	** X	D IX(1) X(1) P=2.0					
50.MYRCIA SP (samples n. 7576 and 7574) - Ripening/ripe fruit Not tested for alkaloids	~XII	S XII evidence from faeces					
51.ZOLLERNIA ILICIFOLIA - Immature seeds Negative for alkaloids	** ~XI	D XI evidence from faeces			D XI evidence from faeces		

52.RHAMNIDIUM ELAEOCARPUM - (Immature?) fruit Not tested for alkaloids	no notes	XII (obs.by R.Mit- termeier)				
53.Malpighiaceae (liana) - Maturing seeds Not tested for alkaloids	no notes	VIII(1)				
54.APARISTHMIUM CORDATUM - Maturing seeds ?	XII & I	XII(1)				
55.CROTON FLORIBUNDUS - Pollen? Flowers?	X	X(1)				
56. - Seeds?	XII & I	XII(1)				
57.CORDIA SELLOWIANA - Ripening fruit?	V & VI	IV(1)				
58.PSIDIUM SP(sample 7546) - Ripe fruit Not tested for alkaloids	?VI to VIII	S VIII evidence from faeces				
59.ATTA SP (Hymenoptera, Formicidae) - Winged females Negative for alkaloids	** ~XI	Obs.by J.C.Ma- galhaes				

(o)- Roman figure: month(s) when item was available/sought
Arabic figure between brackets: the number of 10-min intervals in which at least one animal was seen to consume the item.
D- seeds are destroyed during collection/ingestion
S- seeds recovered from monkey faeces, apparently intact
(?)- uncertain
**- chemical content determined (see table in section I.4.1)
P- "preference" index (see text)

APPENDIX I.3
AVERAGE CHEMICAL COMPOSITION OF SOME PRIMATE/BIRD FOOD ITEMS

All values are percentages of dry weight. "n" is the number of analysed samples used in the averaging (each sample is a different food item). Data from more than one environment.

TYPE OF FOOD	ORIGINAL DATA FROM	CHEMICAL CONSTITUENTS: LIPIDS ("L")	PROTEINS ("P")	CARBOOHYDRATES ("C")	"L"+"P"+"C"
F	C.Hladik, 1978	aver.= 6.6 st.d.= 6.6 n = 12 c.v. = 1.00	aver.= 5.8 st.d.= 2.1 n = 12 c.v.= 0.36	"soluble glucids" aver.= 33.7 st.d.= 17.3 n = 12 c.v.= 0.51	aver.= 46.0 st.d.= 16.4 n = 12 c.v.= 0.36
R U I T S	D.Snow, 1962	"fat" aver.= 28.3 st.d.= 11.9 n = 8 c.v.= 0.42	aver.= 9.5 st.d.= 3.4 n = 8 c.v.= 0.36	(data not available)	(cannot be determined)
(can be an aril, peri-carp, or other part)	D.Snow, 1981	"fat" aver.= 24.8 st.d.= 19.3 n = 20(*) c.v.= 0.78	aver.= 8.9 st.d.= 5.0 n = 20(*) c.v.= 0.56	aver.= 57.3 st.d.= 27.6 n = 12(*) c.v.= 0.48	aver.= 85.2 st.d.= 6.3 n = 12(*) c.v.= 0.07
	H.Howe, ** 1981	54.0 (n=1)	7.0 (n=1)	"usable c/hydrate" 8.0 (n=1)	69.0 (n=1)
	Mc.Diarmid ** 1977	64.0 (n=1)	11.0 (n=1)	"usable c/hydrate" 17.0 (n=1)	92.0 (n=1)
L E A V E S (can be any leaf, shoot, stem, or flush-ing)	C.Hladik, 1978	aver.= 2.3 st.d.= 1.9 n = 10 c.v.= 0.83	aver.= 24.9 st.d.= 13.0 n = 11 c.v.= 0.52	"soluble glucids" aver.= 15.0 st.d.= 7.5 n = 9 c.v.= 0.50	aver.= 38.8 st.d.= 10.8 n = 9 c.v.= 0.27
	A.Hladik, 1978 (mature leaves not included) -Gabon	aver.= 2.9 st.d.= 3.7 n = 13 c.v.= 1.28	aver.= 19.5 st.d.= 13.3 n = 14 c.v.= 0.68	"reducing glucids" aver.= 20.7 st.d.= 7.5 n = 11 c.v.= 0.36	aver.= 39.1 st.d.= 13.7 n = 11 c.v.= 0.35 (not includ. cellulose,~25%)
	-Sri-Lanka	aver.= 3.4 st.d.= 2.4 n = 11 c.v.= 0.70	aver.= 15.6 st.d.= 5.5 n = 11 c.v.= 0.35	"reducing glucids" aver.= 6.6 st.d.= 3.8 n = 11 c.v.= 0.58	aver.= 25.5 st.d.= 6.9 n = 11 c.v.= 0.27 (not includ. cellulose,~19%)

I			"soluble glucids"		
N		aver.= 13.7	aver.= 66.6	aver.= 2.9	aver.= 82.6
S	C.Hladik	st.d.= 9.2	st.d.= 4.0	st.d.= 3.1	st.d.= 7.9
E	1978	n = 3	n = 3	n = 3	n = 3
C		c.v.= 0.67	c.v.= 0.06	c.v.= 1.07	c.v.= 0.10
T					
S	(Under "insects" are included larvae and adults. One of Hladik's samples was a mixture of litter insects)				

(*) - Some of Snow's (1981) samples are the same mentioned in Snow (1962), so the two series of figures are not independent

** - Considered to be one of the richest foods for frugivores (Howe 1981)

c.v.- coefficient of variation

APPENDIX I.4
THE INTEGRATION OF DATA ON GROUP INDEPENDENCE WITH DATA ON THE LOCATION OF GROUPS

DEFINITION OF A CASE

A case is any evidence that there is more than one group (of the same species) in the area. Example of a case: a Cebus group is observed at the hunting hide early in the morning and a group is observed one hour later in a place 600m far from the hide.

INTEGRATION OF CASES

CASE 1

1/1 - The case which indicates the maximum number of independent groups is selected.

1/2 - The location of each independent group is plotted on the map, and a circle is drawn around the location of each group. This circle is named the "home range circle", and its area is equivalent to the average home range area for that species, provided by the literature. (In cases where no information is available for the species, data from another species of the same genus is used.)

1/3 - A straight line is drawn separating adjacent circles, and both lines and circles are identified with the case number. These lines are initially drawn:

1a - with length equal to the diameter of the "home range circle"

1b - midway between the centres of the two adjacent circles

1c - perpendicular to the line linking the centres of the two adjacent circles

but their shape, inclination and position may be later altered to accommodate information from subsequent cases. An alteration is accepted only if, besides accounting for the new information, the new line also separates all the circles that the original line separated.

CASE 2

2/1 - The subsequent case is examined (the sequence is from cases with the largest number of independent groups to those with the smallest).

2/2 - The new simultaneous locations are plotted in the following way:

2/2a - if the new location is contained in an already delimited home range, it is considered as part of that home range, and only a smaller circle (named the "uncertainty circle") is drawn around it. The radius of such circle was (arbitrarily) set at 50m but the accuracy of each plot might be greater or lesser than represented by this circle.

If 2/2a happens and the new location corresponds to a genuinely distinct group, the method will not be able to distinguish between them UNLESS subsequent data indicate such independence.

2/2b - if the new location is outside any previously delimited circle by more than half a "home range circle" radius, a new group is in principle accepted to be there and a new "home range circle" is drawn around it.

If 2/2b happens, this does not necessarily involve the recognition of a new independent group - only if the new location proves independent from the adjacent "home range circles" in subsequent cases.

2/3 - the number of the case is written on the new circles to identify them.

OBS. - If the new case indicates that there is an independent group between two groups previously thought to be adjacent, the lines previously established are re-located in the new three-group model.

2/4 - As in case 1, a line is drawn between the circles of independent groups. Situations possible at this stage are:

2/4a - The independence is already represented by a previously drawn line; the number of the new case is simply added to the line.

2/4b - A previously drawn lines may represent the new case if its position or shape is/are altered; the alteration is made (provided that the new line still accounts for all the previous separations). The case number is added to the altered line, and so are the case numbers of the original line.

A possible alteration of a previously determined line is a change in its shape to fit the outlines of a new 'home-range' circle.

2/4c - None of the previously drawn lines represent the new case - a new separating line is created as in 1/3, and identified by the case number.

CASE 3

A new case is selected and the procedures from 2/1 to 2/4 are repeated until all cases have been examined.

The graphical result is a map containing circles and dividing lines. The reliability of each dividing line is proportional

to the number of cases it is associated with.
The individual circles may be omitted in the final representation, as they were only used to locate the dividing lines and, in fact, the final area ascribed to each group may be quite different from the initial 'home range circle' area.

ASSUMPTIONS OF THE METHOD

The procedure described above assumes:

A- that each group remained in its area, i.e., groups do not move at random across the intensive study area nor enter another group's area.

B- that the study was long and intensive enough to allow all the troops present in the area to have been observed, and information about their independence to be collected.

LIMITATIONS OF THE METHOD

The limitations of the final graphic representation are:

A- the dividing lines are <u>not</u> real home-range boundaries or territory boundaries; they only indicate the existence of independent groups on each side. In several cases, alternative dividing lines (with different shape and position) might explain the observed data equally well. Thus the area defined by the dividng lines does not necessarily correspond to the real home-range area for any troop.

B- if assumption B above is false, the final pattern of spatial distribution is unreliable, and the population size is underestimated.

HOW TO DECIDE WHEN THE METHOD IS INAPPROPRIATE

If a given group enters areas previously occupied by other groups, the alteration of dividing lines may be insufficient to account for all the evidence. If a single instance goes against a line that is supported by several other cases, the line may be maintained and a "reversal" is accepted. If the reversals approach the number of consistent cases, the method is inappropriate.

APPENDIX I.5

Cebus apella and *Brachyteles arachnoides* (Cebidae)

as potential pollinators of *Mabea fistulifera* (Euphorbiaceae)

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CEBUS APELLA AND *BRACHYTELES ARACHNOIDES* (CEBIDAE) AS POTENTIAL POLLINATORS OF *MABEA FISTULIFERA* (EUPHORBIACEAE)

Primates occasionally visit flowers of certain plants without destroying them, suggesting that the primates might be acting as pollinators. Sussman (1979) noted that *Lemur mongoz* and *Microcebus murinus* (Lemuridae) licked the nectar produced by *Ceiba pentandra* (Bombacaceae), and mentioned other instances in which both lemurs and lorises possibly acted as pollinators. In the New World, Oppenheimer (1968, 1977) indicated *Cebus capucinus* was a possible pollinating agent for *Ochroma pyramidale* (Bombacaceae). Sussman and Raven (1978) considered this to be the only documented case of a monkey acting as an important pollinating agent.

This note describes another instance in which New World primates seem to be acting as pollinators. The observations were made during 1979 at Barreiro Rico (Estado de São Paulo), Brazil. The area contains *Cebus apella, Callicebus personatus, Brachyteles arachnoides, Alouatta fusca,* and *Callithrix jacchus* (=*C. aurita*). I observed *C. apella* and *B. arachnoides* visiting the inflorescences of *Mabea fistulifera* (Euphorbiaceae). Trees of this species attain heights of 10 to 15 m, and flower from February to June, with a flowering peak in April. The inflorescences are terminal, numerous, and strongly scented. Each has about 300 male flowers and three to six female flowers. The latter are clustered at the base of the inflorescence (Fig. 1).

Other animals observed at the inflorescences were *Apis mellifera* (Hymenoptera: Apidae), *Trigona* sp. (Hymenoptera: Apidae), an unidentified ant, and a hummingbird. Although ants and hummingbirds did not seem to touch the anthers, the bees did collect and carry pollen from *Mabea* anthers. I could not discern whether the bees contacted the stigmas. Janzen (1975:20) stated that "from the plant's viewpoint, most of the social bees are a detrimental component in the ecosystem. They are primarily flower visitors rather than pollinators."

Sussman and Raven (1978) and Sussman (1979) suggested that primates may be pollinators in circumstances where the pollinating agents that coevolved with the plant are absent. In the cases Sussman (1979) studied, he thought it unlikely that coevolution between plants and primates as pollinators had occurred, because the primates were visiting plants that were normally pollinated by bats. I could not determine if bats visited *Mabea fistulifera*, so the possibility that the inflorescences are pollinated by bats (or other nocturnal animals) remains to be checked. Nonetheless, *C. apella* and *B. arachnoides* certainly behaved like pollinators and the characteristics of the plant seem to be conducive to that. The distinctive pink to maroon and strongly scented flowers may provide locator cues for the primates. The flowers produce copious nectar during a period when there are not many fruits or seeds available. In turn, the primates visit many *Mabea* trees per day, become covered with pollen, and their activity is not generally destructive to the flowers. However, their interaction with *Mabea* is not always beneficial because they may also reduce the reproductive potential of *Mabea* later in the season. *C. capucinus* destroys the fruits of *M. occidentalis* to eat the seeds (Oppenheimer, 1968, in press; Hladik and Hladik, 1969). Similarly, *C. apella* ate the maturing seeds of *M. fistulifera* at Barreiro Rico during August and September. The monkeys did not deplete the seed stock; many *Mabea* seeds were visible on the forest floor in mid-September.

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Literature Cited

Hladik, A., and C. H. Hladik. 1969. Rapports trophiques entre vegetation et primates dans la forêt de Barro Colorado (Panama). La Terre et la Vie, 23:27–117.

Janzen, D. H. 1975. Ecology of plants in the tropics. Studies in biology. Edward Arnold Ltd., London, 58:1–66.

Oppenheimer, J. R. 1968. Behavior and ecology of the white-faced monkey *Cebus capucinus* on Barro Colorado Island. Unpubl. Ph.D. dissert., Univ. Illinois, Urbana, 179 pp.

———. 1977. Forest structure and its relation to activity of the capuchin monkey (*Cebus*). Pp. 74–84, *in* Use of non-human primates in biomedical research (M. R. N. Prasad and T. C. A. Kumar, eds.). Indian Nat. Sci. Acad., New Delhi, 426 pp.

———. In press. *Cebus capucinus*: home range, population dynamics and interspecific relationships. *In* The ecology of a Neotropical forest: seasonal rhythms and long-term changes (E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, eds.). Smithsonian Press, Washington, D.C.

Sussman, R. W. 1979. Nectar feeding by prosimians and its evolutionary and ecological implications. Pp. 569–577, *in* Primate ecology: problem-oriented field studies. John Wiley and Sons, New York, 596 pp.

Sussman, R. W., and P. H. Raven. 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. Science, 200:731–736.

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APPENDIX I.6

Descrição das matas da Fazenda Barreiro Rico,

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Descrição das matas da Fazenda Barreiro Rico, Estado de São Paulo

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ABSTRACT – (Description of the forests of Barreiro Rico Farm, São Paulo State). A description of the forests of Barreiro Rico Farm (Município de Anhembi, Estado de São Paulo) is presented, with emphasis on the tree component. Three environments are identified, on the basis of the presence of exclusive and selective species, and also by their characteristic physiognomies. These different environments are dependent on the relief, but probably reflect the interaction among several factors such as soil conditions, frost and fire. The floristic composition of Barreiro Rico forest is compared with that of other Brazilian forests and with a Panamanian one. Data on the time of flowering and fruiting of about 50 tree species are also given.

RESUMO – (Descrição das matas da Fazenda Barreiro Rico, Estado de São Paulo). Apresenta-se uma descrição das matas da Fazenda Barreiro Rico, Município de Anhembi, Estado de São Paulo, focalizando-se principalmente o componente arbóreo. Identificam-se três ambientes distintos, caracterizados pela ocorrência de espécies exclusivas e seletivas, e também por fisionomias características. A separação dos ambientes está relacionada com a topografia, mas provavelmente reflete a interação entre diversos fatores como condições edáficas, geadas e queimadas. A composição florística das matas de Barreiro Rico é comparada com a de outras formações florestais do Brasil e com uma do Panamá, ao nível genérico. São fornecidos dados de floração e frutificação de cerca de 50 espécies arbóreas.

Key words: forests, Barreiro Rico Farm.

Introdução

Esta primeira descrição da vegetação natural da Fazenda Barreiro Rico foi feita como parte de um estudo sobre ecologia e comportamento dos primatas ali presentes. O objetivo era retratar, ainda que preliminarmente, a fisionomia da vegetação, sua composição florística e comportamento fenológico.

A fazenda Barreiro Rico é uma propriedade particular localizada pouco acima da confluência dos rios Piracicaba e Tietê (hoje represados pela barragem de Barra Bonita), no Município de Anhembi, Estado de São Paulo. A área atualmente coberta por vegetação original é de 2200ha, divididos em três blocos (de 326, 488 e 1386ha). Originalmente a mata era extensa e abrangia ambientes ripários (rios mencionados acima), porém foi sendo progressivamente reduzida devido a necessidades da fazenda. Em 1963 somou-se a isso a inundação provocada pelo enchimento da represa de Barra Bonita, que cobriu boa parte dos ambientes ripários ainda existentes. A figura 1 mostra a localização exata dos blocos de mata atuais, e sua altitude.

O tipo de clima da região é CwA no sistema de Koeppen. Como ali a precipitação sobrepuja a evapotranspiração, há no solo um fluxo de água de cima para baixo que tende a lixiviá-lo (Setzer 1966). Os meses de menor precipitação são julho-agosto (nos últimos 19 anos a média de precipitação nesses dois meses combinados foi 69mm); o máximo de precipitações ocorre em dezembro-janeiro (a média de precipitação desses dois meses combinados foi, nos últimos 19 anos, 411mm). Segundo o Atlas Pluviométrico do Estado de São Paulo (1972), as maiores diferenças entre médias de precipitação de dois meses consecutivos ocorrem entre março e abril (diminuição nas precipitações) e entre setembro e outubro (aumento nas precipitações). Monteiro (1976) caracteriza a área onde está Barreiro Rico da seguinte forma: existência de período seco, média anual de umidade relativa do ar entre 70 e 75%, média anual de temperatura entre 18 e 22°C, sem deficiência de água no período mais seco, média de 15 dias de instabilidade por mês.

A região abrange arenitos do Grupo Botucatu (Triássico). Segundo a "Carta de solos da Fazenda Barreiro Rico" (Ranzani & Pessotti 1975), o solo da área coberta por matas é homogêneo e constituído por areias quartzosas.

Métodos

Esta descrição é uma primeira aproximação e será aprofundada através de estudo fitossociológico em execução por um dos autores. Esta primeira fase foi executada em uma área de estudo intensivo constituída por cerca de 115ha de matas e cerca de 4ha de formação aberta (ver figura 2). Ocasionalmente foram feitas coletas fora dessa área, principalmente de espécies não encontradas na área de estudo intensivo.

A presente descrição baseou-se em:

Amostragem das espécies presentes – Sempre que alguma espécie produzia estruturas reprodutivas, procurava-se coletar uma amostra desse material. Desenhos e observações sobre cor, agentes polinizadores, localização do indivíduo (ou outras) eram feitas no campo, no instante da coleta. O material coletado era então preservado, etiquetado e posteriormente identificado. Isto foi feito durante estadias na mata de no mínimo oito dias completos por mês, durante todo o ano de 1979. Embora esse sistema de amostragem permita teoricamente abranger todas as espécies, isto na verdade não ocorreu. Além das espécies cuja floração ou frutificação passaram desapercebidas, algumas espécies (reconhecíveis pelas partes vegetativas) não produziram estruturas reprodutivas durante 1979 (ou as produziram por um período muito curto) e não foram, portanto, incluídas na amostra. Além disso, não foi possível obter amostras de todas as espécies que foram observadas em floração. Parte do material obtido encontra-se depositado no herbário da Universidade Estadual de Campinas (UEC). Uma coleção completa foi mantida pela primeira autora como coleção de referência.

Etiquetagem de indivíduos – Sempre que se reconhecia uma espécie de árvore ou arbusto, procurava-se etiquetar pelo menos dez indivíduos dessa espécie, à medida que

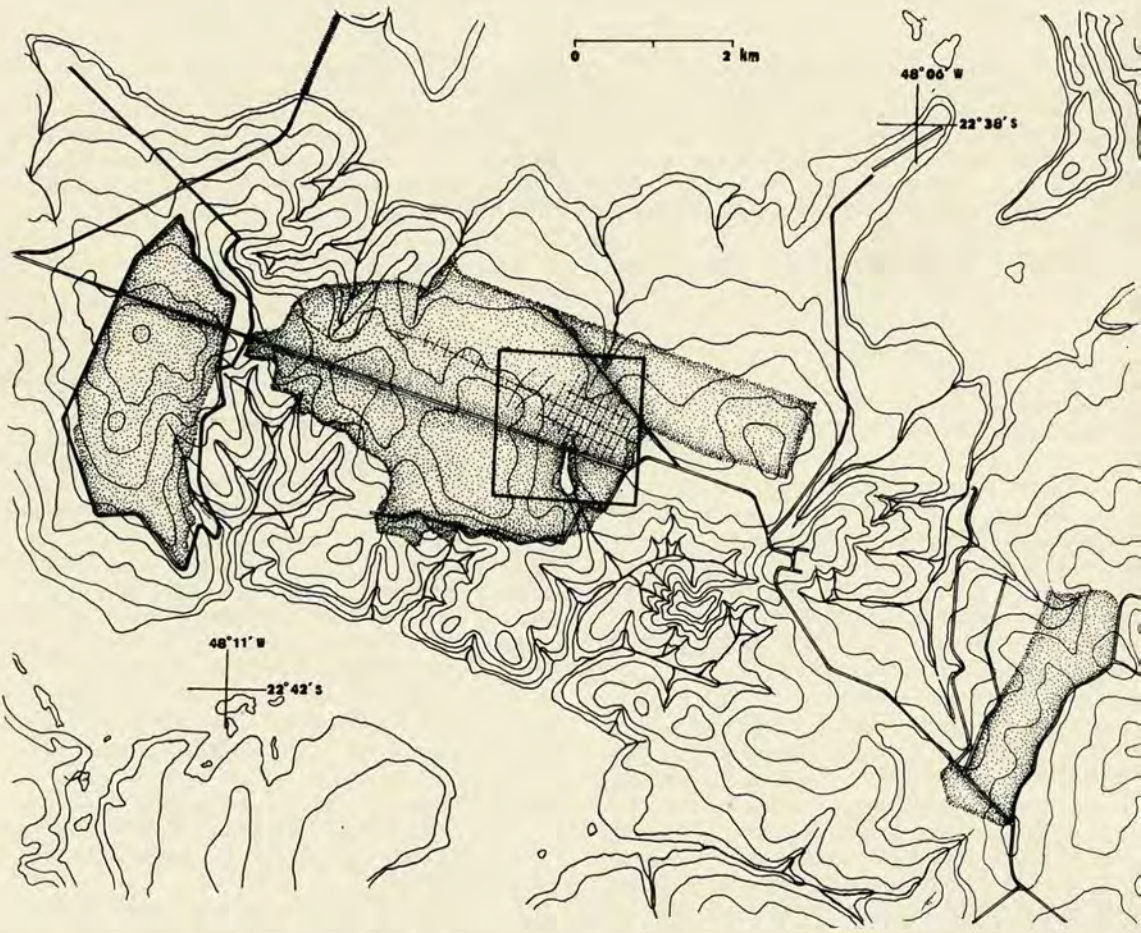


Figura 1. Localização dos blocos de mata de Barreiro Rico (sombreado). O quadrado indicado com linha grossa corresponde à área retratada na figura 2. Equidistância das curvas de nível: 20 metros. (baseado no mapa IBGE 1:50.000, folha Santa Maria da Serra, 1974)

iam sendo notados na mata. Nem sempre foi possível encontrar dez indivíduos da espécie. Freqüentemente essa etiquetagem era feita na época da floração da espécie, aproveitando sua maior conspicuidade. As árvores etiquetadas eram também plotadas em mapa. A finalidade da etiquetagem era permitir acompanhar o ciclo fenológico de cada espécie através de uma amostra de vários indivíduos a serem observados mensalmente. Esse exame não foi, porém, regular; parte dos dados fenológicos aqui apresentados foram obtidos através de: a) datas de coleta de material reprodutivo; b) anotações feitas ao longo do ano com base em indivíduos não necessariamente etiquetados e c) notas tomadas no momento da etiquetagem. Através desse sistema de marcação individualizaram-se cerca de 320 indivíduos de 70 espécies de angiospermas.

Transetos de vegetação – Cada transeto consistia numa faixa de 100 x 2,5m. Todos os indivíduos de pelo menos 10cm de DAP. enraizados nessa área, foram identificados e representados em perfis. Os perfis foram feitos em papel milimetrado, e as dimensões das árvores foram determinadas com trena e um clinômetro de fabricação caseira. Executaram-se três transetos, um em cada tipo de vegetação reconhecido. Sua localização é indicada na figura 2. A finalidade dos transetos era: a) reproduzir, por meio de desenhos, a fisionomia da mata, uma vez que a visualização da fisionomia é freqüentemente impossível em campo (Aubréville 1965); b) permitir um exame preliminar da composição florística dos vários ambientes reconhecidos.

Espécies presentes em Barreiro Rico

Resultados obtidos – Entre janeiro de 1979 e janeiro de 1980 foram reconhecidas e amostradas 158 espécies de angiospermas, pertencentes a 55 famílias, sendo 76 espécies arbóreas, 38 arbustivas, 21 trepadeiras, 16 herbáceas e 7 epífitas. É certo que esses valores não representam a totalidade das espécies, particularmente no que diz respeito às de menor porte. Na tabela 1 listamos as espécies amostradas. Acreditamos que a maior parte das espécies lenhosas existentes na área de estudo intensivo (cerca de 115ha) tenha sido amostrada, pois, tomando por referência a lista de madeiras de Barreiro Rico (amostras colecionadas ao longo de muitos anos pelos proprietários da fazenda), apenas cerca de dez madeiras não foram incluídas na nossa amostra. Como a maior parte dessas espécies parece ser mais encontradiça em áreas da fazenda com solos não arenosos, ou ainda em áreas desmatadas (pastos), dificilmente as encontraríamos na área de estudo intensivo. Essas espécies, que sabidamente ocorrem em Barreiro Rico, mas que não foram amostradas durante o estudo, não estão sendo consideradas neste trabalho.

Discussão – Admitindo que o conjunto de espécies arbóreas amostradas represente uma aproximação razoável da composição real, tentamos uma comparação entre nossa área de estudo e ou-

Tabela 1. Espécies amostradas em Barreiro Rico. a – árvores; s – arbustos; t – trepadeiras; h – herbáceas; e – epífitas; ma – espécie encontrada na mata; fa – espécie encontrada na formação aberta

ACANTHACEAE
Ruellia sp (h, ma)

ANACARDIACEAE
Astronium graveolens Jacq. (guaritá) (a, ma)

APOCYNACEAE
Aspidosperma nemorale Handro (guatambu) (a, ma)
Aspidosperma peroba Saldanha da Gama (peroba) (a, ma)
Condylocarpum sp (t)
Mandevilla sp (t)
Peschiera fuchsiaefolia (.dc.) Miers (leiteira da invernada) (s)

ANNONACEAE
Annona cacans Warm. (araticum) (a, ma)
Duguetia furfuracea (St. Hil.) Benth. & Hook. (pinha do cerrado) (s, fa)
Duguetia lanceolata St. Hil. (pindaíba) (a, ma)
Guatteria sp (t)
Xylopia brasiliensis Spreng. (erva-doce) (a, ma)

AQUIFOLIACEAE
Ilex cerasifolia Lam. (a, ma)

ARACEAE
Philodendron sp (imbe) (t, ma)

ARALIACEAE
Didymopanax morototoni Decne. & Planch. (mandioqueiro) (a, ma)
Didymopanax vinosum (Cham. & Sch.) March (s, fa)

BIGNONIACEAE
Adenocalymma sp (t)
Anemopaegma sp (t)
Arrabidaea sp (t)
Callychlamys sp (t)
Fridericia speciosa Mart. (t)
Lundia sp (t)
Melloa quadrivalvis (Jacq.) A. Gentry (t)
Pithecoctenium sp (pente de macaco) (t)
Pyrostegia venusta Miers (flor de S. João) (t)
Stizophyllum perforatum Miers (t)
Tabebuia vellosoi Toledo (am. 7555) (ipê) (a, ma)
Zeyhera tuberculosa (Vell.) Bur. (bolsa de pastor, (a,ma)

BORAGINACEAE
Cordia ecalyculata Vell. (café de bugre) (a, ma)
Cordia sellowiana Cham. (açuquinha da mata) (a, ma)

CARICACEAE
Jacaratia spinosa (Aublet) A. DC. (jaracatiá) (a, ma)

CELASTRACEAE
Maytenus sp (am. 7571, 7589) (a, ma)

continua

Tabela 1. Espécies amostradas em Barreiro Rico. a – árvores; s – arbustos; t – trepadeiras; h – herbáceas; e – epífitas; ma – espécie encontrada na mata; fa – espécie encontrada na formação aberta (continuação)

COMPOSITAE
Baccharis dracunculifolia DC. (alecrim do campo) (s, fa)
Calea clausseniana Baker (h, fa)
Gochnatia pulchra Cabr. (s, fa)
Piptocarpha macropoda (DC.) Baker
Vernonia cognata Less. (h, fa)
Vernonia scorpoides (Lam.) Pers. (h,fa)

CUNONIACEAE
Lamanonia glabra Camb. (a, ma)

CYPERACEAE
Rhynchospora exaltata Kunth. (navalha de macaco) (h)

DIOSCOREACEAE
Dioscorea sp (t)

ELAEOCARPACEAE
Sloanea monosperma Vell. (bugreiro, ouriço) (a, ma)

ERYTHROXYLACEAE
Erythroxylum campestre St. Hil. (a, fa)
Erythroxylum pelleterianum St. Hil. (s, fa)

EUPHORBIACEAE
Actinostemon estrellensis (Muell. Arg.) Pax (pau de espeto (s, ma)
Alchornea triplinervia Muell. Arg. (tapiazeiro) (a, ma)
Aparisthmium cordatum Baill. (boleiro) (a, ma)
Croton floribundus Spreng. (capexingui) (a, ma)
Gonatogyne brasiliensis Muell. Arg. (guaraiúva branca) (a, ma)
Mabea fistulifera Mart. (canudeira-de-pito, leiteira-do-mato) (a, ma)
Pachystroma illicifolium (Klotzch.) Muell. Arg. (canxim) (a, ma)
Pera obovata Baill. (a, ma)
Sebastiania sp 1 (am. s/n) (h, fa)
Sebastiania sp 2 (am. s/n) (a, ma)
Securinega guaraiuva Kuhlm. (guaraiúva) (a, ma)

FLACOURTIACEAE
Casearia inaequilatera Camb. (guassatonga) (a, ma)

GRAMINEAE
Merostachys sp (taquari) (ma)
Ichnanthus sp (h, ma)

GUTTIFERAE
Rheedia gardneriana Planch. & Triana (a, ma)

ICACINACEAE
Villaresia sp (am. 7569) (a, ma)

LAURACEAE
Cryptocaria moschata Nees et Mart. (batalheira, canela-batalha) (a, ma)
Nectandra sp (canela cheirosa) (a, ma)
Ocotea acutifolia (Nees.) Mez. (canela preta) (a, ma)
Ocotea aff. *spixiana* (Nees.) Mez. (canelão) (am. 7528) (a, ma)
Ocotea pulchella Mart. (s, fa)

LECYTHIDACEAE
Cariniana estrellensis (Raddi) O. Kuntze (jequitibá) (a, ma)

LEGUMINOSAE
Acacia plumosa Lowe (cipó de espinho) (t)
Acacia polyphylla DC. (monjoleiro, gorocaia) (a, ma)
Bauhinia sp (t)
Cassia aff. *rugosa* (s, fa)
Copaifera langsdorfii Desf. (pau de óleo) (a, fa & ma)
Dalbergia variabilis Vog. (t)
Dioclea sp (cipó coronha) (t)
Hymenaea courbaril L. (jatobá) (a, ma)
Inga striata Benth. (inga) (a, ma)
Stryphnodendron adstringens (Mart.) Colville (barbatimão) (a, fa)
Zollernia ilicifolia Vog. (pau jantar) (a, ma)

LOGANIACEAE
Strychnos brasiliensis Mart. (salta martí) (s)
Strychnos sp (h, fa)

LORANTACEAE
(não identificada) (am. 7536) (e)

MAGNOLIACEAE
Talauma ovata St. Hil. (pinha do brejo) (a, ma)

MALPIGHIACEAE
Byrsonima intermedia A. Juss. (s, fa)
Heteropteris sp (t)
(não identificada) (am. s/n) (t)

MELASTOMATACEAE
Miconia albicans (Sw.) Triana (s)
Miconia candolleana Triana (s, ma)
Miconia fallax DC. (s)
Miconia langsdorfii Logn. (h)
Miconia sp (am. 7552) (a, ma)
Mouriri sp (am. 7521) (pitanga brava) (a, ma)
(não identificada) (am. 7553) (s)
(não identificada) (am. 7560) (h)

MONIMIACEAE
Siparuna sp (limão bravo do mato) (am. 7522) (s, ma)

MORACEAE
Cecropia hololeuca Miq. (embaúba) (a, ma)
Ficus sp (figueira) (e)

MYRSINACEAE
Rapanea guyanensis Aublet (am. 7545) (carne de vaca) (a, ma)
Rapanea lancifolia (Mart.) Mez (s, fa)

MYRTACEAE
Blepharocalyx sp (s, fa)
Callyptrogenia sp (am. 7563) (piúna) (a, ma)
? *Campomanesia* (am. 7578) (s, fa)
Eugenia pyriformis Camb. (uvaia) (a, ma)

continua

Tabela 1. Espécies amostradas em Barreiro Rico.
a – árvores; s – arbustos; t – trepadeiras; h – herbáceas; e – epífitas; ma – espécie encontrada na mata; fa – espécie encontrada na formação aberta (continuação)

Eugenia sp (am. 7517) (a, ma)
Eugenia squamulosa Mattos (s, ma)
Gomidesia sp 1 (am. 7524) (brasa viva) (a, ma)
Gomidesia sp 2 (am. 7530) (a, ma)
Myrcia obtecta (Berg.) Kiaersk. (s)
Myrcia formosiana DC. (am. 7520) (a, ma)
Myrcia sp 1 (am. 7574) (s, fa)
Myrcia sp 2 (am. 7576) (s, fa)
Myrcia sp 3 (am. s/n) (s, fa)
Myrciaria sp (am. 7532) (cambuí) (a, ma)
Myrceugenia sp (am s/n) (a, fa)
Psidium sp (am. 7546, 7559) (a, ma)

OCHNACEAE
Ouratea salicifolia Engl. (a, ma)

OPILIACEAE
Agonandra brasiliensis Miers (a, ma)

PALMAE
Syagrus campestris (Mart.) Wendl. (h, fa)
Syagrus sp (am. s/n) (coqueiro) (a, ma)

PHYTHOLACACEAE
Seguieria langsdorfii Mog. (t)

PIPERACEAE
Ottonia sp (am. 7564) (s, ma)
Peperomia sp (e, ma)
Piper sp (am. 7585) (s, ma)

POLYGONACEAE
Coccoloba sp (am. 7579) (taxi, taxizeiro) (a, ma)

PROTEACEAE
Roupala sp (am. s/n) (a, ma)

RHAMNACEAE
Rhamnidium elaeocarpum Reiss. (saguaragi amarelo) (a, ma)

RUBIACEAE
Alibertia sp (am. 7519) (s, ma)
Amaioua guianensis Aublet (a, ma)
Chiococca brachiata Ruiz & Pav. (t)
Faramea sp (am. 7544) (s, ma)
Palicourea rigida H.B.K. (h)
Palicourea sp (h, ma)
Psychotria vauthieri Muell. Arg. (am. 7558) (a, ma)
Psychotria sp 1 (am. 7565) (a, ma)
Psychotria sp 2 (am. s/n) (h, ma)
Psychotria sp 3 (am. 7535, 7582 (pipoca) (h, ma)
Tocoyena formosa (Cham. & Sch.) K. Sch. (s, fa)

RUTACEAE
Esenbeckia febrifuga A. Juss (mamoninho) (s, ma)
Esenbeckia intermedia Mart. (canela de cotia) (a, ma)
Esenbeckia leiocarpa Engl. (guarantã) (a, ma)
Galipea jasminiflora Engl. (mamoninha) (a, ma)
Metrodorea nigra St. Hil. (carrapateira) (a, ma)
Pilocarpus pauciflorus St. Hil. (amendoim torrado) (a, ma)
Zanthoxylum rhoifolium Lam. (mamica de porca) (a, ma)

SAPINDACEAE
Cupania sp (am. 7557) (arco de peneira) (s, ma)
Paullinia sp (t)
Serjania sp (t)

SAPOTACEAE
Chrysophyllum gonocarpum (Mart. et Eichl.) Engl. (a, ma)

SOLANACEAE
Solanum megalochiton Mart. (s, ma)
Solanum sp 1 (am. 7587) (s, ma)
Solanum sp 2 (am. s/n) (jurubéba) (s, ma)
Solanum swartzianum Roem. et Schutz (folha de prata) (s, ma)

STERCULIACEAE
Guazuma ulmifolia Lam. (coração de negro) (a, ma)

TILIACEAE
Prockia crucis L. (a, ma)

ULMACEAE
Celtis spinosa Spreng. (galinha choca) (a, ma)

VERBENACEAE
Aegiphila sp (s)
Lippia sp (h)

VIOLACEAE
Hybanthus atropurpureus Taub. (h)

VOCHYSIACEAE
Vochysia tucanorum Mart. (cinzeiro) (a, ma)
Qualea jundiahy Warm. (pau terra, goiaba do mato) (a, ma)

tras matas das quais se conhece a composição florística. Essa comparação foi feita a nível de gênero. Nossa amostra inclui 65 gêneros arbóreos. A tabela 2 mostra o número de gêneros em comum com outras áreas de composição florística conhecida.

Ao examinar a tabela 2, é preciso levar em conta que nem todos os estudos nela citados foram executados segundo os mesmos métodos. Por exemplo, tanto o diâmetro mínimo considerado como o número total de árvores examinadas variaram de estudo para estudo. As diferenças de método e esforço por certo estão refletidas nos valores das colunas 3 e 4. Apesar disso, esses valores revelam um padrão consistente com as classificações propostas para as matas do sul do Brasil por Aubréville (1961) e por Klein (1975).

A coluna 4 da tabela 2 mostra o número de gêneros em comum entre Barreiro Rico e as várias localidades consideradas. Esses valores não são, no

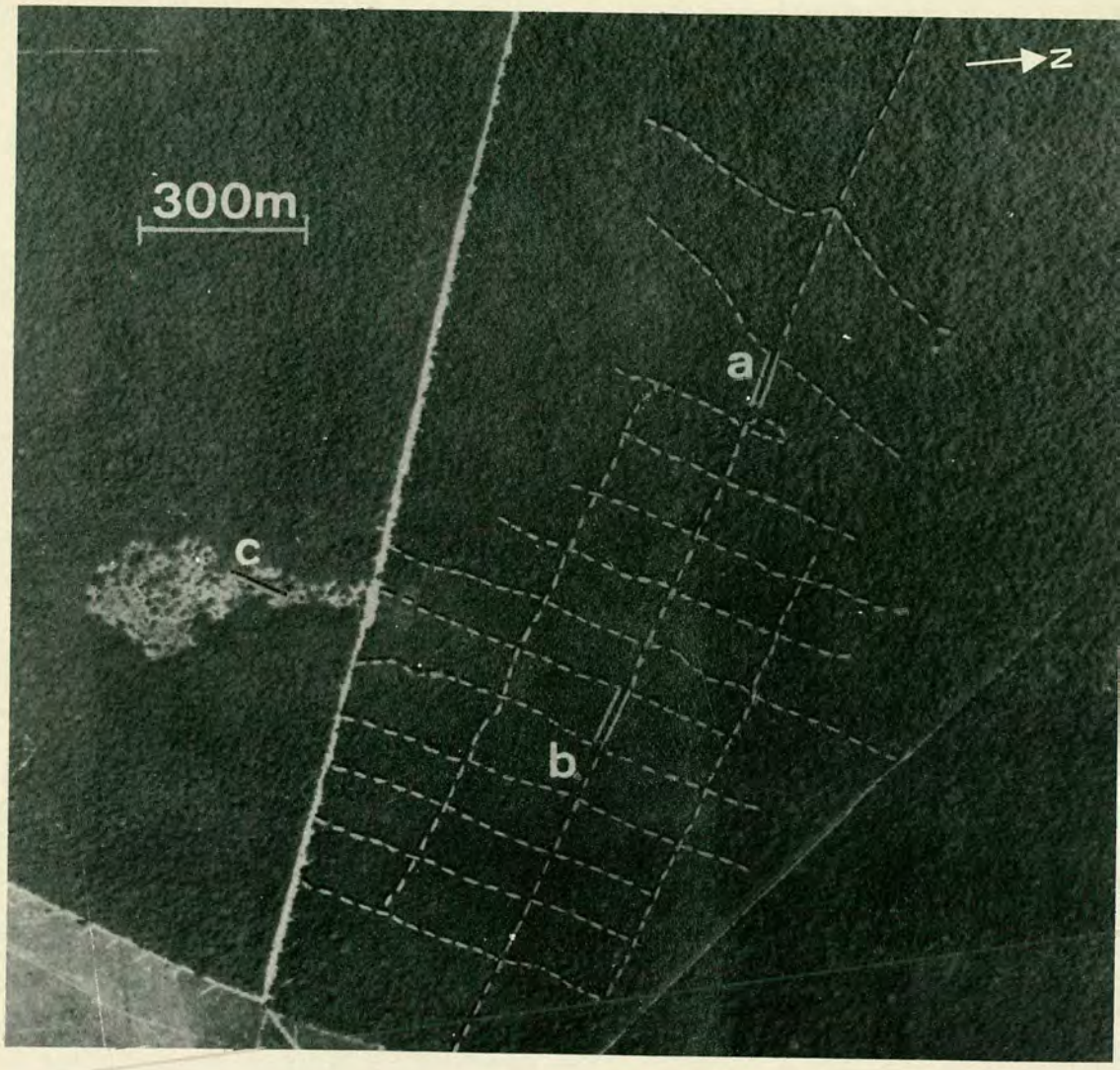


Figura 2. Fotografia aérea da área de estudo intensivo. Os segmentos *a*, *b* e *c* indicam a localização dos transetos mencionados no texto. As linhas tracejadas são trilhas. Notar a área de formação aberta, nitidamente destacada da mata.

entanto, a melhor indicação de afinidade, pois o número de gêneros em comum é função do número total de gêneros amostrados nas localidades em questão. Uma medida mais aceitável de afinidade é dada pela coluna 5, cujos valores são a relação entre número de gêneros em comum às duas áreas e o número total de gêneros dessas mesmas áreas. A ordenação dos valores da coluna 5 é, no entanto, semelhante à dos valores da coluna 4, de modo que, embora o número de gêneros observados nas várias localidades varie bastante (por exemplo, 112 gêneros em Jequitibás contra 70 em Capetinga), isso não chega a mascarar a seqüência de afinidade.

Notamos, na tabela 2, que a afinidade decresce, a grosso modo, com a distância existente entre as matas consideradas. As matas do oeste amazônico e a do Panamá tem os menores valores de afinidade com Barreiro Rico. Em seguida, os menores valores são os das demais matas amazônicas e as do Brasil central, seguidos dos da mata Atlântica. É interessante notar que o valor de afinidade de Guamá com B. Rico parece superior aos das

matas do Brasil central e próximo ao da mata Atlântica da costa. Esse padrão é razoável se pensarmos que Guamá fica mais próxima da conexão mata Atlântica-mata amazônica que as demais matas amazônicas. Além disso, o estudo feito em Mocambo (Black *et al.* 1950) não é tão preciso quanto o feito em Guamá (Pires *et al.* 1953), que portanto deve representar melhor a vegetação do leste amazônico. Infelizmente, os valores da coluna 5 são muito semelhantes entre si, não permitindo muita resolução entre as várias localidades. Apesar disso, é notável a tendência de aumento de afinidade à medida em que se consideram localidades mais próximas de Barreiro Rico, principalmente Capetinga, Morro do Diabo, Cantareira, Mogi-Guaçu e Jequitibás. A maior afinidade entre essas áreas seria esperada, pois essas localidades, assim como Barreiro Rico, pertenceriam ao conjunto de florestas da bacia do rio Paraná, tanto segundo a classificação de Aubréville (1961) como segundo a de Klein (1975). Apenas surpreende o fato de Cantareira estar em posição de maior afinidade com Barreiro Rico do que a mata Capetinga, já que, além de Capetinga estar mais próxima geograficamente de Barreiro Rico do que está Cantareira, esta última atinge cotas bem superiores (mais de 1000 metros) às das duas outras localidades (em torno de 500 metros). Esperaríamos que Canta-

Tabela 2. Comparação dos gêneros que ocorrem em B. Rico com os que ocorrem em outras localidades. (Baseada em 65 gêneros arbóreos amostrados em B. Rico)

Local	Estudo por	Nº total de gêner. arbóreos	Nº de gên. em comum com B.R.	Nº de gên. em comum com B.R. / Nº total de gên. nas duas localidades (**) X 100
Terra firme, Tefé (AM)	Black *et al.* (1950)	41	8	8.2
Flor. trop. úmida do Panamá	Golley *et al.* (1978)	153	19	8.7
Terra firme, Mocambo (PA)	Black *et al.* (1950)	65	12	10.2
Floresta seca Xav./ Cachimbo (MT)	Ratter *et al.* (1973)	25	9	11.1
Solos mesotróficos, Brasil central	Ratter *et al.* (1978 B) (*)	91	18	13.0
Terra firme, Manaus-Itacoatiara (AM)	Prance *et al.* (1976)	115	21	13.2
Floresta seca de Suiá-Missu (MT)	Ratter *et al.* (1978 A)	33	12	13.9
Mata primária de Teresópolis (RJ)	Veloso (1945)	36	13	14.8
Terra firme, Guamá (PA)	Pires *et al.* (1953)	111	23	15.0
Fazenda Comari (RJ)	Davis (1945)	54	17	16.7
Mata Capetinga (SP)	Martins (1979)	70	24	21.6
Morro do Diabo (SP)	Campos & Heinsdijk (1974)	55	24	25.0
Cantareira (SP)	Negreiros *et al.* (1974)	48	23	25.5
Mata ciliar de Mogi-Guaçu (SP)	Gibbs & Leitão Filho (1978)	53	24	25,5
Bosque dos Jequitibás (SP)	Matthes (1980)	112	37	26.4

(*) Ratter *et al.* (1978 B) consideraram "espécies lenhosas", e não árvores, o que não permite comparação rigorosa.
(**) O denominador é calculado somando-se o número de gêneros presentes em Barreiro Rico ao número de gêneros da localidade em questão e subtraindo-se o número de gêneros em comum.

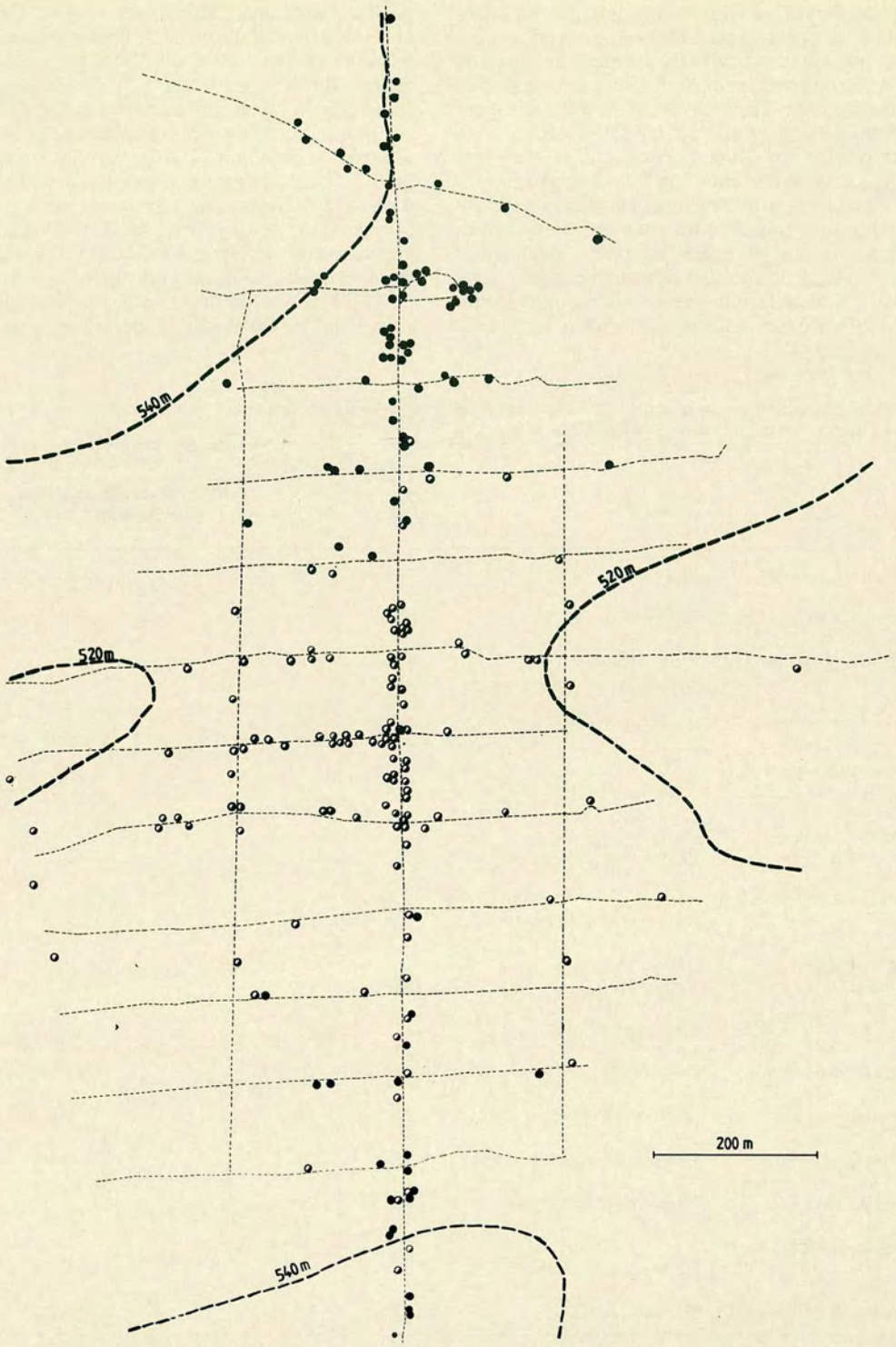


Figura 3. Distribuição das árvores e/ou arbustos pertencentes a espécies não indiferentes. Cada círculo representa um indivíduo etiquetado. Círculos negros: espécies típicas do ambiente "A". Círculos claros: espécies típicas do ambiente "B".

reira fosse uma transição entre matas de planalto e de serra. A sua inclusão entre as matas de maior afinidade com Barreiro Rico pode não ser um reflexo da realidade, mas um efeito de amostragem. Enquanto o estudo de Martins (1979) seguiu uma metodologia rigorosa e considerou árvores com DAP de 4,8 cm, o estudo de Negreiros *et al.* (1974), é preliminar, tendo focalizado apenas árvores de grande porte. O número de gêneros presentes em Cantareira deve ser bem superior ao indicado. A diferença de método nesses dois estudos certamente influiu nos resultados obtidos, e pode ser responsável pela discrepância mencionada.

É conveniente lembrar que o sistema utilizado para estimar afinidades deu igual importância a todos os gêneros, ou seja, não se consideraram diferenças na abundância relativa dos vários gêneros. Em princípio, a inclusão de muitos gêneros raros poderia mascarar a importância de espécies dominantes em comum, de modo que o índice utilizado não é uma indicação perfeita de afinidade, e deve ser sempre usado com cautela.

Tabela 3. Exemplos de espécies indiferentes e de espécies não indiferentes

Ambiente	Espécies não indiferentes	Espécies indiferentes
A + B		*Aspidosperma nemorale* (Apocyn.) *Gonatogyne brasiliensis* (Euphorb.) *Actinostemon estrellensis* (Euphorb.) *Alchornea triplinervia* (Euphorb.) *Cryptocarya moschata* (Laur.) *Ocotea acutifolia* (Laur.) *Hymenaea courbaril* (Legum.) *Qualea jundiahy* (Vochys.)
A + B + C		*Copaifera langsdorfii* (Legum.)
A	*Aspidosperma peroba* (Apocyn.) *Securinega guaraiuva* (Euphorb.) *Nectandra* sp (canela-cheirosa) (Laur.) *Zollernia ilicifolia* (Legum.) *Pachystroma illicifolium* (Euphorb.) *Callyptrogenia* sp (piuna) (Myrt.) *Psychotria* sp (7565) (Rub.) *Esenbeckia leiocarpa* (Rut.) *Pilocarpus pauciflorus* (Rut.) *Galipea jasminiflora* (Rut.) *Metrodorea nigra* (Rut.)	
B	*Annona cacans* (Annon.) *Duguetia lanceolata* (Annon.) *Cordia sellowiana* (Borag.) *Maytenus* sp (7571) (Myrt.) *Mabea fistulifera* (Euphorb.) *Pera obovata* (Euphorb.) *Miconia candolleana* (Melast.) *Eugenia* sp (7517) *Psidium* sp (7546) (Myrt.) *Myrcia formosiana* (7520) (Myrt.) *Amaioua guyanensis* (Rub.)	
C	*Duguetia furfuracea* (Annon.) *Didymopanax vinosum* (Aral.) *Ocotea pulchela* (Laur.) *Stryphnodendron adstringens* (Legum.) *Byrsonima campestre* (Malp.) *Byrsonima intermedia* (Malp.) *Miconia fallax* (Melast.) *Rapanea lancifolia* (Myrs.) *Myrcia* spp (7574, 7576) (Myrt.) *Blepharocalyx* sp (Myrt.) *?Campomanesia* sp (7578) (Myrt.)	

Distribuição espacial das espécies

Resultados – Nem todas as espécies distribuem-se da mesma forma pela área de estudo. Algumas parecem indiferentes, sendo encontradas por toda a área de estudo intensivo, mas outras são encontradas preferencialmente em algumas zonas. Na tabela 3 listam-se as espécies mais seletivas. Algumas delas são na verdade exclusivas (estenotópicas), ou seja, ocorrem apenas num tipo de ambiente. Através da localização dos indivíduos dessas espécies não indiferentes, identificamos três ambientes: A – "alto", B – "baixada" e C – "cerrado". Os ambientes A e B correspondem as matas propriamente ditas, enquanto C corresponde a uma formação aberta que se assemelha fisionomicamente a um cerrado (nitidamente destacado da mata, ver figura 2). A figura 3 mostra, na região de matas propriamente ditas, a localização das árvores e arbustos etiquetados que pertencem a espécies não indiferentes. A distribuição dessas espécies indica dois tipos de mata, representados na figura por círculos claros e círculos escuros. Os círculos claros representam espécies encontradas quase que exclusivamente no ambiente B, e estão concentradas na parte central da figura. Os círculos escuros representam espécies típicas do ambiente A. Nota-se que na parte superior da figura os círculos escuros não se misturam com os círculos claros, enquanto que na parte inferior há essa mistura. As cotas nas duas áreas de transição A/B são aproximadamente as mesmas. A mistura de espécies na parte inferior da figura pode ser devida ao fato de que essa parte do desenho corresponde à zona mais alterada da área de estudo intensivo (essa é a área mais visitada, pois a estrada que percorre a mata inicia-se ali; as árvores de maior porte dessa zona foram abatidas). A instalação de espécies típicas do ambiente B nessa região pode ser devida à colonização de espaços alterados.

Os três ambientes identificados (A,B,C) foram representados em perfis (Figura 4). Nos perfis A e B representaram-se todas as plantas com pelo menos 10cm DAP. Em C, porém, como as várias espécies lenhosas ramificam-se praticamente ao nível do solo, assumindo aspecto arbustivo, representamos no perfil todas as plantas com pelo menos 10cm de diâmetro a qualquer altura. Ao examinar esses perfis, devemos nos lembrar que eles não incluem o sub-bosque, que era característico para cada ambiente (em C não se aplica o conceito de sub-bosque). Em B, a mata era particularmente densa, em parte devido à existência, nessa área, de grande quantidade de touceiras de taquari *(Merostachys)*.

A composição florística dos três ambientes, amostrada através da identificação dos indivíduos presentes nos três transetos da figura 2, indicou que as três áreas parecem ser bastante diferentes também na composição. Os dados são apresentados na tabela 4, onde notamos que cada ambiente é caracterizado por uma família que predomina em número de indivíduos. Interessantemente, a razão entre número de espécies e número de indivíduos

Tabela 4. Comparação da composição florística dos transetos

Ambiente	Famílias mais comuns	% do total de indivíduos do transeto	Espécies envolvidas	Espécies no transeto	Nº espécie / Nº indivíd
A	Rutac.	15/29=52%	*Esenbeckia leiocarpa* *Pilocarpus pauciflorus* *Metrodorea nigra* *Galipea jasminiflora*	12	0.41
	Melast.	05/29=17%	*Mouriri* sp (7521)		
B	Euphor.	18/38=47%	*Mabea fistulifera* *Aparisthmium cordatum* *Croton floribundus* *Gonatogyne brasiliensis*	20	0.53
	Myrt.	06/38=16%	*Gomidesia* sp 1 (7524) *Gomidesia* sp 2 (7530) *Myrcia formosiana* *Eugenia* sp (7517) *Myrciaria* sp (7532)		
C	Legum.	06/14=43%	*Stryphnodendron adstringens* *Copaifera langsdorfii*	07	0.50
	Myrt.	04/14=29%	*Blepharocalyx* sp *Myrcia* spp (7575, 7574)		

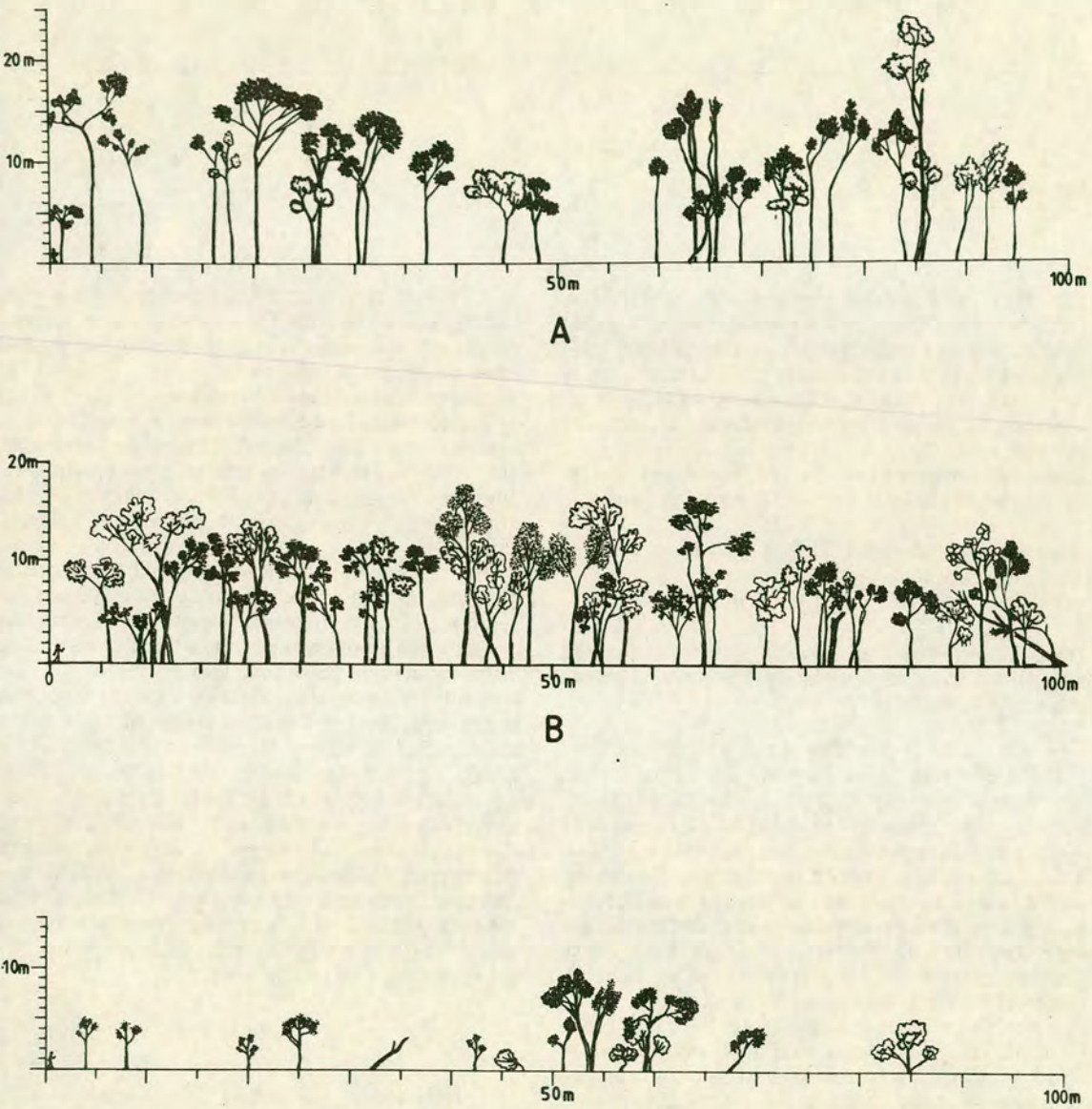


Figura 4. Perfis de vegetação efetuados nos três ambientes reconhecidos. Para A e B estão representadas todas as plantas com pelo menos 10cm de D.A.P. Para C, todas as plantas com pelo menos 10cm a qualquer altura. Nos perfis, a faixa considerada tinha 2,5 x 100m.

Tabela 5. Floração de espécies ao longo do ano. Em cada célula está indicado o número de espécies em flor. Valores dentro de um círculo estão significativamente acima (dois desvios-padrão) da média da linha. Pontos de interrogação indicam casos sobre os quais não dispomos de informação (nesses casos o valor deve ser próximo de zero). Parênteses indicam que a informação não provém de observação direta (por exemplo, uma informação dada por moradores).

Spp. do ambiente \ Mês	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
A	2	3	1	0	0	2	2	1	⑥	3	2	2	22
B	2	2	3	1	3	1	0	3	5	⑧	2	1	29
C	0	0	0	0	2	?	0	0	?	⑤	,0	1	8
Spp indif.	0	0	1	1	(1)	0	0	1	5	5	3	3	20

por área, uma medida grosseira de diversidade (última coluna da tabela 4) assume valores semelhantes nos três ambientes. É preciso, porém, lembrar que nossa amostra é bastante reduzida.

Nos três ambientes há uma substituição de espécies do mesmo gênero. Podemos citar como exemplos:

Duguetia furfuracea em C – *D. lanceolata* em B
Ocotea pulchella em C – *O. acutifolia* em A e B
Rapanea lancifolia em C – *R. guyanensis* em A
Didymopanax vinosum em C – *D. morototoni* em A e B

Há ainda uma substituição mais complexa, nos três ambientes, entre as espécies de *Psychotria, Myrcia, Eugenia* e *Miconia.*

Discussão – Acredita-se que a vegetação tipo C tenha evoluído como resposta a um solo arenoso, presumivelmente distrófico, sem distinção de horizontes até mais de 7 metros (J.C.R. Magalhães, com. pess.). Porque a floresta tipo B está contígua à formação aberta (tipo C), e porque, da mesma forma que C, B ocupa uma área limitada, a floresta tipo B deve também estar associada com condições específicas de solo. No entanto, B não é um mero ecótone entre A e C. B parece ser um ambiente à parte; B contém muitas espécies exclusivas, e as espécies tipicamente encontradas em A e em C não se misturam em B, o que seria de se esperar caso B fosse um simples ecótone. Mesmo fisionomicamente B não pode ser considerado intermediário entre A e C. O ambiente C parece ser hostil. Nessa área, mesmo as espécies "indiferentes" não atingem o tamanho que atingem em A ou em B. Em C as poucas árvores presentes estão agrupadas, formando aglomerados de árvores em meio a arbustos de pequeno porte e herbáceas. Nesses aglomerados, a própria forma das árvores sugere competição por manchas de solo. Por outro lado, B tem, dentre os três ambientes, a maior densidade de árvores, e também o sub-bosque mais denso.

Vimos que a separação dos ambientes está associada à topografia. Pelo menos quatro fatores associados à topografia poderiam estar envolvidos nessa distinção de ambientes:

– profundidade do lençol freático.
– disponibilidade de nutrientes. É possível que haja diferenças na disponibilidades de nutrientes nos vários ambientes, associada a uma estrutura diferente de solo em cada área. Infelizmente não dispomos de dados detalhados sobre o solo desses ambientes.
– fogo. Há relatos de moradores e outras evidências não publicadas de que teria ocorrido um incêndio na área da baixada. Alguns estudiosos consideram que a presença de taquari nessa área é uma indicação de que sua vegetação foi alterada.
– geada. A região das matas de Barreiro Rico está sujeita a geadas, que afetam principalmente áreas mais baixas. Estas geadas poderiam estar selecionando espécies mais resistentes. Dentre as espécies em que notamos perda de folhas após geada citamos *Gonatogyne brasiliensis, Mabea fistulifera, Aparisthmium cordatum, Stryphnodendron adstringens, Alchornea triplinervia* e *Ocotea* aff. *spixiana.* Nos casos de *Mabea* e de *Ocotea* aff. *spixiana* a produção de frutos das árvores atingidas parece ter sido comprometida, dada a queima das inflorescências do fim da floração.

Fenologia

Resultados – A tabela 5 indica que os três ambientes têm um comportamento fenológico ligeiramente diferente: a região A floresce predominantemente em setembro, enquanto B e C florescem predominantemente em outubro.

A tabela 6 fornece dados fenológicos de parte do componente arbóreo de Barreiro Rico (ano de 1979). Na confecção da tabela 6 omitiram-se as espécies sobre as quais obteve-se pouca informação, seja pela raridade da espécie seja pelo espaçamento das observações.

Tabela 6. Floração e frutificação de algumas espécies arbóreas de B. Rico durante 1979. A informação entre parênteses não provém das anotações de campo: é apenas uma ligação lógica das informações dos meses adjacentes. Células em branco não indicam ausência de observações, mas a não constatação de estruturas reprodutivas. FT – frutos maduros; FL – flores abertas; ft – frutos em formação; fl – flores em formação.

Espécie	Meses											
	J	F	M	A	M	J	J	A	S	O	N	D
Esenbeckia leiocarpa		ft	ft	(ft)	ft	(ft)	FT	FT	FT	fl	FT	FL
Cryptocarya moschata	FT	FT	FT						fl	(fl)	ft	FT
Annona cacans	FT	FT							FL	FL	ft	ft
Croton floribundus	FT									FL	ft	FT
Securinega guaraiuva	(ft)	(ft)	FT	FT		FT	FT		FL	ft	ft	ft
Gonatogyne brasiliensis	FT	FT	FT				fl	(fl)	FL	FL	ft	FT
Pilocarpus pauciflorus		FL	FL	(ft)	(ft)	ft	(ft)	(ft)	ft			
Galipea jasminiflora	FL	FL	(ft)	ft	ft	FT						fl
Vochysia tucanorum	FL	FL	FL		FL			ft				fl
Mabea fistulifera	fl	FL	FL	FL	FL	ft	ft	ft	FT	FT		
Eugenia sp (am. 7517)	ft	FT	FT									?fl
Myrcia formosiana	ft	FT								fl	FL	ft
Mouriri sp (am. 7521)		ft		ft	ft	ft		ft	FT	FT		?fl
Qualea jundiahy	(ft)	(ft)	ft	(ft)	ft	(ft)	ft	(ft)	FT	FL	FL	(ft)
Gomidesia sp (am. 7524)	(ft)	(ft)	FT								FL	(ft)
Pera obovata			FL		FL		ft	ft	FT	(FT)	FT	
Alchornea triplinervia			FL		ft					ft	FT	FT
Ocotea spixiana				FL	FL	ft	(ft)	FT	FT	FT	FT	
Hymenaea courbaril				ft	ft	ft	FT	FT	fl	FL		
Ilex cerasifolia			ft	(ft)	(ft)	FT				FL		
Myrciaria sp (am. 7532)												fl
Aparisthmium cordatum	FT									FL	ft	FT
Cordia sellowiana				ft	FL ft							
Sloanea monosperma						ft	ft	FT	FT			
Copaifera langsdorfii	(ft)	(ft)	(ft)	(ft)	ft	FT	FT	FT				FL
Psidium sp (am. 7546)						FT	FT	FT fl				ft
Agonandra brasiliensis							FL					
Duguetia lanceolata	ft	FT					fl	(fl)	FL	FL		ft
Metrodorea nigra	(ft)	FT					fl	fl	FL	(ft)	(ft)	(ft)
Miconia sp (7552)		fl					FT	FT				
Astronium graveolens								FL	FL ft	ft	ft	
Eugenia pyriformis									FL FT	FT		
Callyptrogenia sp									FL			
Aspidosperma nemorale									FL	(ft)	ft	FT
Villaresia sp									FT			
Xylopia brasiliensis									FT fl	FT FL	FL	FL
Maytenus sp (am. 7571)										FL	(ft)	ft
Ouratea salicifolia										FL	(ft)	ft
Coccoloba sp (7579)										FL	ft	ft
Amaioua guianensis											FL	
Zollernia ilicifolia										FL	FT	
Ocotea acutifolia											fl	FL
Didymopanax morototoni	FL ft									fl	(fl)	FL ft
Inga striata	ft	FT						fl	FL	FL	(ft)	FT
Aspidosperma peroba	ft	(ft)									FL ft	ft
Pachistroma illicifolium	ft	FT								fl		
Esenbeckia intermedia	FT											FL
Psychotria sp (am. 7565)	FT	FT							FL	(ft)	ft	FT

Discussão – A tabela 6 mostra que a maior parte das espécies amadurece seus frutos na estação chuvosa ou no fim da estação seca. Os frutos maduros da estação seca correspondem em geral a estruturas secas (por exemplo, em *Esenbeckia, Securinega, Copaifera*). A tabela 6 mostra também que várias espécies protelam o amadurecimento de seus frutos por muitos meses (*Xylopia* e *Qualea* sendo bons exemplos). Esses fatos, e também a perda total de folhas por algumas espécies no fim da estação seca (por exemplo *Hymenaea, Copaifera, Aspidosperma nemorale*) sugerem que o "stress" hídrico é importante em Barreiro Rico. O solo arenoso provavelmente intensifica as condições da estação seca.

Agradecimentos – Expressamos nosso reconhecimento a Dr. José Carlos Reis de Magalhães, que não só permitiu o acesso às matas da fazenda Barreiro Rico como estimulou e facilitou a execução dos trabalhos. Alguns dos dados citados na introdução deste artigo chegaram-nos por seu intermédio. C.T.A. recebeu apoio financeiro das seguintes instituições: FAPESP – Fundação de Amparo à Pesquisa do Estado de São Paulo, CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Fauna Preservation Society (Londres) e New York Zoological Society.

Referências

AUBRÉVILLE, A. 1961. *Étude écologique des principales formations végétales du Brésil.* UNESCO e Centre National de la Recherche Scientifique (CNRS), Nogent-sur-Marne.

AUBRÉVILLE, A. 1965. Principes d'une systématique des formations végétales tropicales. *Adansonia* 5: 153-196.

BLACK, G.A., DOBZHANSKY, T., PAVAN, C. 1950. Some attempts to estimate species diversity and population density of trees in Amazonian forest. *Botanical Gazette* 111: 413-425.

CAMPOS, J.C.C. & HEINSDIJK, D. 1974. A floresta do Morro do Diabo. *Silvic. S. Paulo* 7: 45-58 *apud* Coimbra-Filho, A.F. 1976. *Leontopithecus rosalia chrysopygus,* o mico-leão do Estado de São Paulo. *Silvic. S. Paulo* 10: 1-36.

DAVIS, D.E. 1945. The annual cycle of plants, mosquitos, birds and mammals in two Brazilian forests. *Ecol. Monogr.* 15: 245-295.

GIBBS, P.E. & LEITÃO FILHO, H.F. 1978. Floristic composition of an area of gallery forest near Mogi-Guaçu, State of São Paulo, SE Brazil. *Revta brasil. Bot.* 1: 151-156.

GOLLEY, F.B., MCGINNIS J.T., CLEMENTS, R.G., CHILD, G.I. & DUEVER, M.J. 1978. *Ciclagem de minerais em um ecossistema de floresta tropical úmida.* Editora Pedagógica e Universitária, São Paulo.

KLEIN, R.M. 1975. Southern Brazilian phytogeographic features and the probable influence of upper Quaternary climatic changes in the floristic distribution. *Boletim Paranaense de Geociências* 33: 67-88.

MARTINS, F.R. 1979. *O método de quadrantes e a fitossociologia de uma floresta residual do interior do Estado de São Paulo: Parque Estadual de Vassununga.* Tese de Doutoramento, Instituto de Biociências, Universidade de São Paulo, São Paulo

MATTHES, L.A.F. 1980. *Composição florística, estrutura e fenologia de uma floresta residual do planalto paulista: Bosque dos Jequitibás (Campinas, SP).* Dissertação de Mestrado, Instituto de Biologia, Universidade Estadual de Campinas, Campinas

MONTEIRO, C.A.F. 1976. O clima e a organização do espaço no Estado de São Paulo: problemas e perspectivas. Instituto de Geografia da Universidade de São Paulo. *Série Teses e Monografias* nº 28, São Paulo.

NEGREIROS, O.C., CARVALHO, C.T., CESAR, S.F., DUARTE, F.R., DESHLER, W.O., THELEN, K.D. 1974. Plano de manejo para o Parque Estadual da Cantareira. Instituto Florestal, *Boletim Técnico* nº 10, São Paulo.

PIRES, J.M. DOBZHANSKY, T., BLACK, G.A. 1953. An estimate of the number of trees in an Amazonian forest community. *Botanical Gazette* 114: 467-477.

PRANCE, G.T., RODRIGUES, W.A., SILVA, M.F. 1976. Inventário florestal de um hectare de mata de terra firme, Km 30 da estrada Manaus-Itacoatiara. *Acta Amazonica* 6: 9-35.

RANZANI, G. & PESSOTTI, J.E. 1975. Carta de solos da Fazenda Barreiro Rico, Cia. Itaquerê Industrial e Agrícola (1:25000, 1528 ha).

RATTER, J.A., RICHARDS, P.W., ARGENT, G. & GIFFORD, D.R. 1973. Observations on the vegetation types of northeastern Mato Grosso. I. The woody vegetation types of the Xavantina-Cachimbo expedition area. *Phil. Trans. Royal Soc. London, Biological*

RATTER, J.A., ASKEW, G.P., MONTGOMERY, R.F. & GIFFORD, D.R. 1978 A. Observations on the vegetation of northeastern Mato Grosso. II. Forests and soils of the rio Suiá-Missu area. *Proc. R. Soc. Lond. B* 203: 191-208.

RATTER, J.A., ASKEW, G.P., MONTGOMERY, R.F & GIFFORD, D.R. 1978 B. Observations on forests of some mesotrophic soils in central Brazil. *Revta brasil. Bot.* 1: 47-58.

SÃO PAULO. 1972. *Atlas Pluviométrico do Estado de São Paulo.* Departamento de Águas e Energia Elétrica, Centro Tecnológico de Hidráulica, São Paulo

SETZER, J. 1966. *Atlas Climático e Ecológico do Estado de São Paulo.* Comissão Interestadual da Bacia do Paraná e Centrais Elétricas de São Paulo, São Paulo

VELOSO, H.P. 1945. As comunidades e as estações botânicas de Teresópolis, Estado do Rio de Janeiro. *Bol. Mus. Nac. Bot.* 3: 1-95.

APPENDIX I.7
USE OF THE AREA BY THE PRIMATES: DETAILS OF THE METHOD USED

ESTIMATE OF SAMPLING BIAS

As mentioned in section I.3.1.3, my presence in a given part of the study area depended on the existence of trails there. The various trails were built at different times during the study, so some hectares were more visited than others. This called for a correction of the raw data. The real frequency with which I visited each hectare was not measured, but it should be proportional to the accessibility of each hectare. This accessibility can be estimated from the number of trails leading to each hectare and the length of time when these trails were available. As the trails were cut to form a grid dividing the area into 1-ha quadrats, the accessibility of each quadrat can be estimated by adding, for each month, the number of quadrat sides that corresponded to trails, and then adding the monthly totals for the whole study period. In part of the intensive study area (see top of following figures) the trails were cut by another researcher and did not form a grid. For this area the monthly counts considered the number of trails that either crossed or bordered a given 1-ha quadrat. The totals for each quadrat are an accessibility index. These totals are shown in a transparency (page 302) placed over a trail map to show the correspondence between the trails and the quadrats.

MEASURES USED TO INVESTIGATE USE OF HOME RANGE

For Callicebus, Callithrix and Alouatta I used the number of independent encounters occurred in each quadrat to measure relative use of quadrats. (Not all encounters were used; cases in which an animal left the previous night was followed the following morning cannot be considered independent encounters). Each encounter corresponded to one score, placed at the hectare where the group was first seen in that encounter. For the more mobile species, Cebus and Brachyteles, encounters generally provided more information about movement across the home range; to make maximal use of this information, instead of considering only the initial location of the group, I divided the period of the encounter into intervals and for each interval a score was given to each quadrat entered by the troop. For Cebus the interval was fixed at 19 minutes and for Brachyteles at 16 minutes, since this was how long each species took (on average) to cross a quadrat. If after this interval an animal was still in the same quadrat, it could be said to have chosen to remain there, and the quadrat received a new score. When the animals were between quadrats, the scores were divided among the quadrats involved.

RAW DATA ON THE PRIMATES LOCATION

The data on the number and location of encounters (scores) are available in Fig.I.13 (Callicebus), Fig.I.15 (Callithrix), Fig.I.18

(Alouatta), and in the following pages(303/06) for Brachyteles and Cebus. The Cebus data are restricted to the three troops that were observed more frequently.

CORRECTION OF DATA FOR DIFFERENTIAL SAMPLING

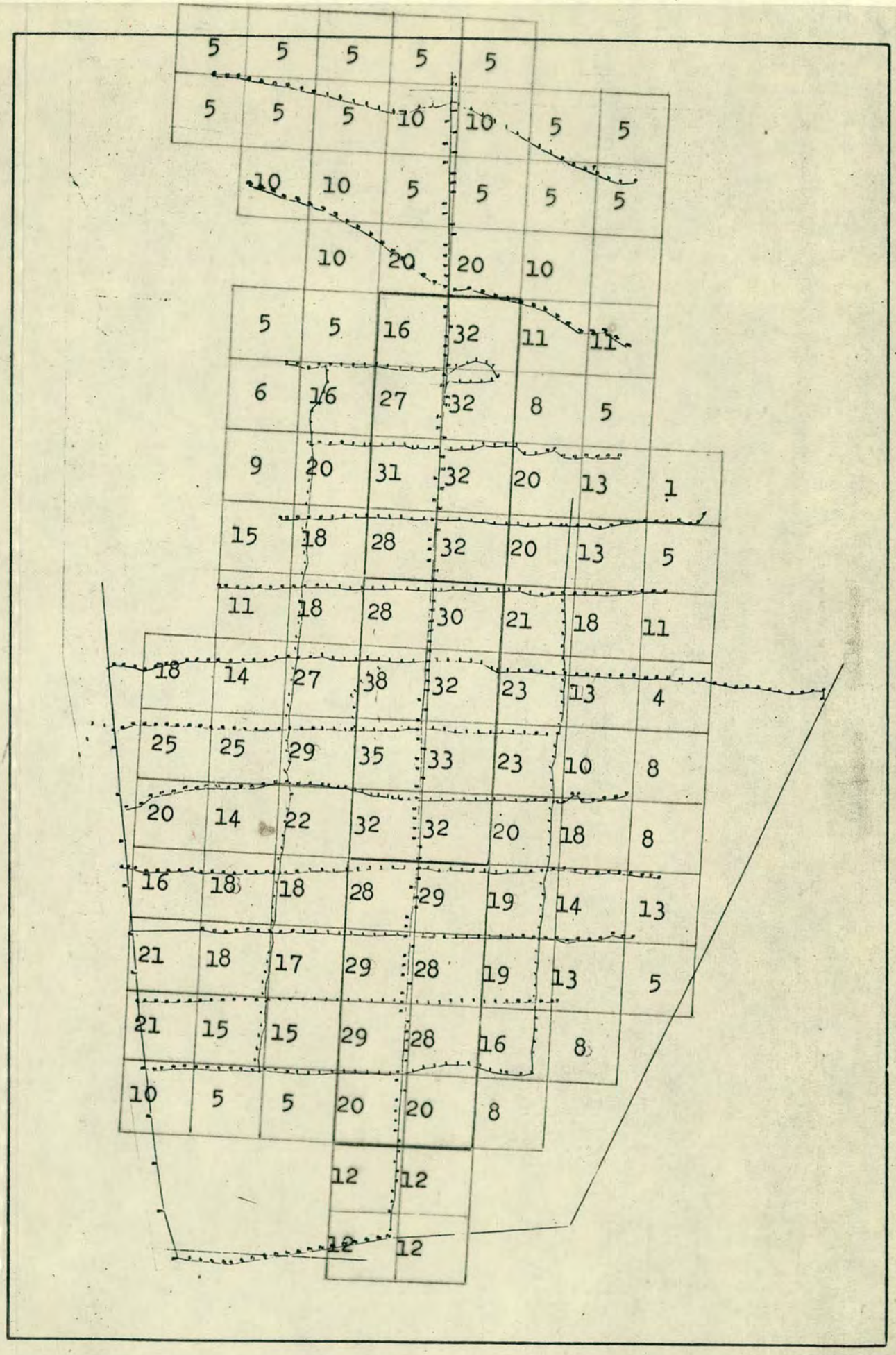
For Callicebus, Callithrix and Alouatta, the accessibility indexes were used to calculate the expected number of scores of each quadrat in the following way:

$$\text{Expected n.scores in quadrat A} = \frac{\text{total n.scores in all quadrats}}{\text{sum of acces.indexes of all quad.}} \times \text{access. index of quad. A}$$

For Cebus a similar formula was used, but only the quadrats actually seen to be entered by the animals were considered. For Brachyteles the expected value was extrapolated from a regression line of average scores over classes of accessibility indexes ($r=0.84$, $n=7$).

For all species except Cebus, the number of scores in each quadrat is very low. Assuming that in any quadrat the number of scores follows a Poisson distribution, the expected number of encounters can be used to determine the probability associated with the real number of scores. For Cebus the Poisson distribution was not used and I merely identified those quadrats where the deviation from expected was highest. (The results obtained for each species are presented under the heading "Use of home range" in sections I.3.3, I.3.4, I.3.5, I.3.6 and I.3.7).

To check whether the scores observed were indeed following a Poisson distribution, a chi-square test was done on the Brachyteles data for (a) the only large set of quadrats that had exactly the same accessibility index; (b) on several classes of accessibility index (each class containing 5 consecutive indexes). In 4 out of 6 tests the observed scores could be said to fit a Poisson distribution.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5 5 5 10 10 5 5
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6 16 27 32 8 5
9 20 31 32 20 13 1
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11 18 28 30 21 18 11
18 14 27 38 32 23 13 4
25 25 29 35 33 23 10 8
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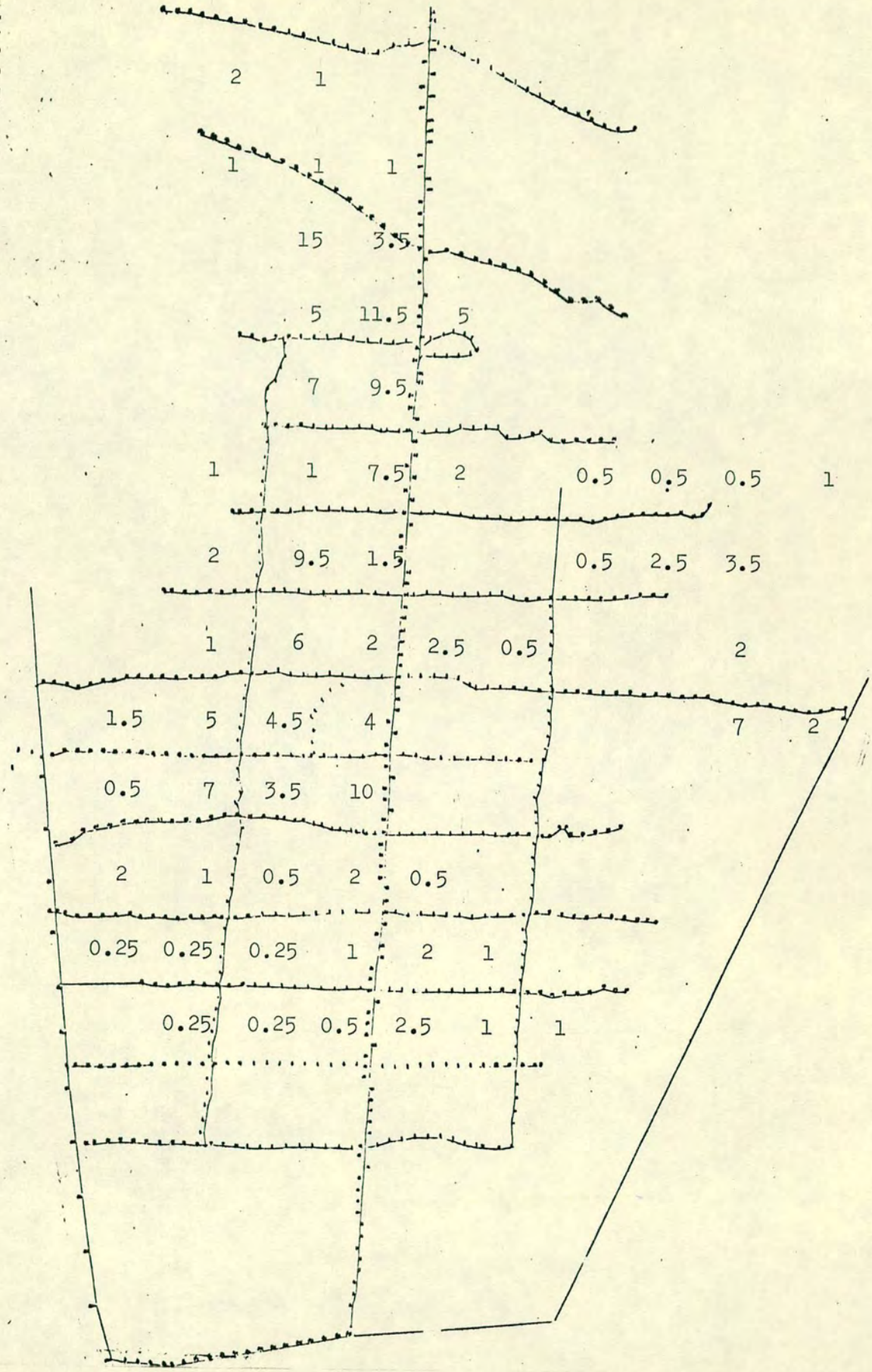
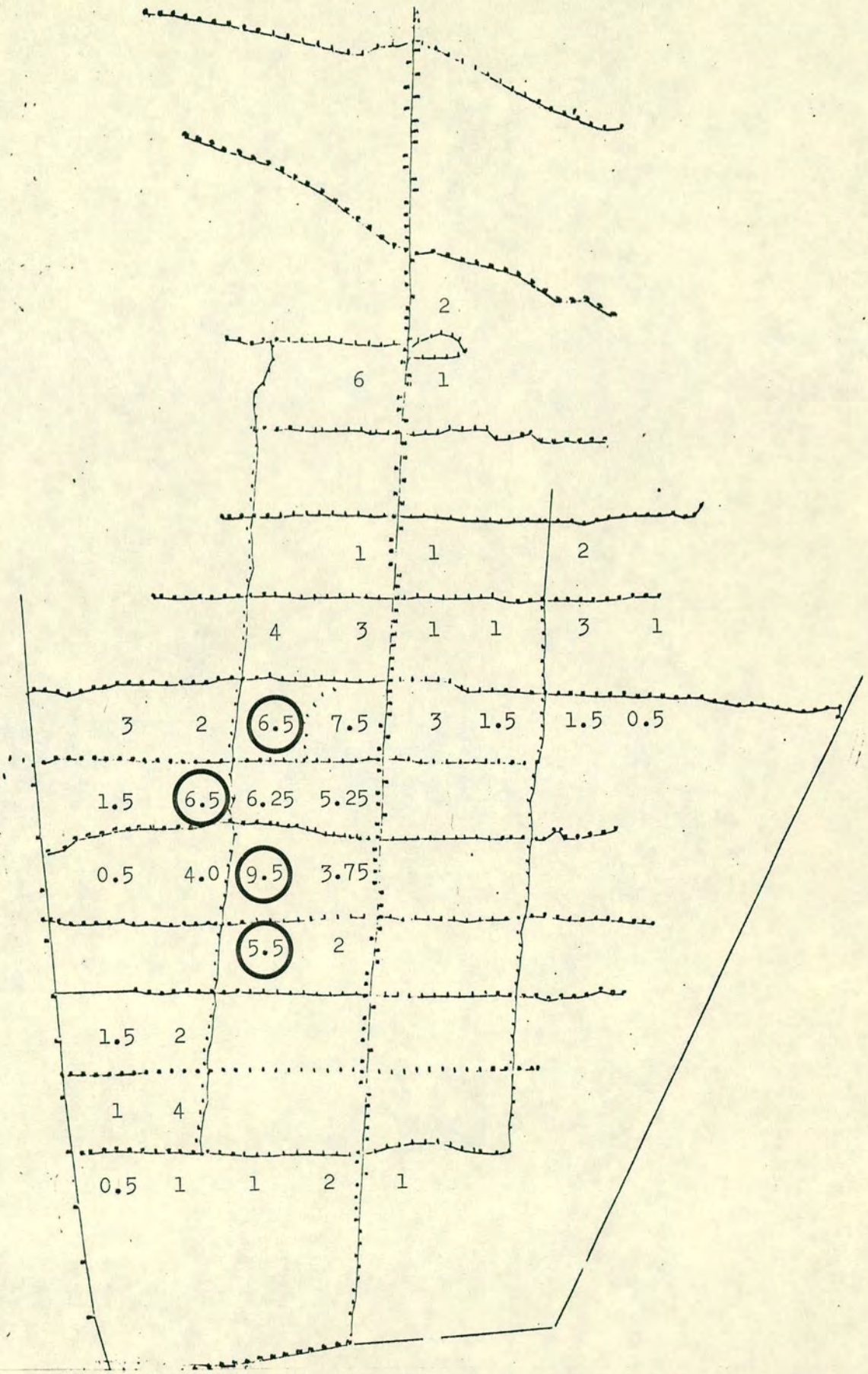
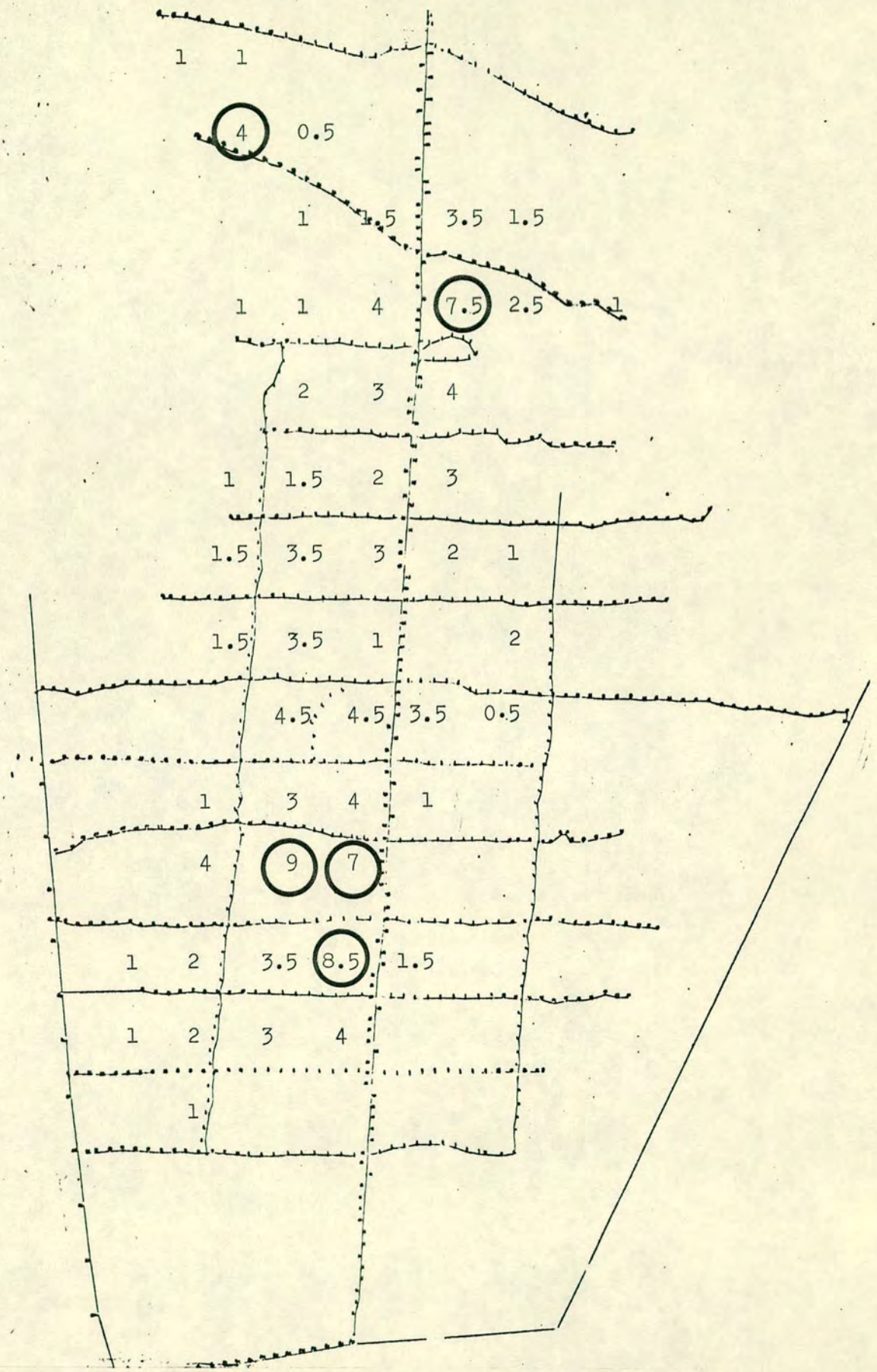


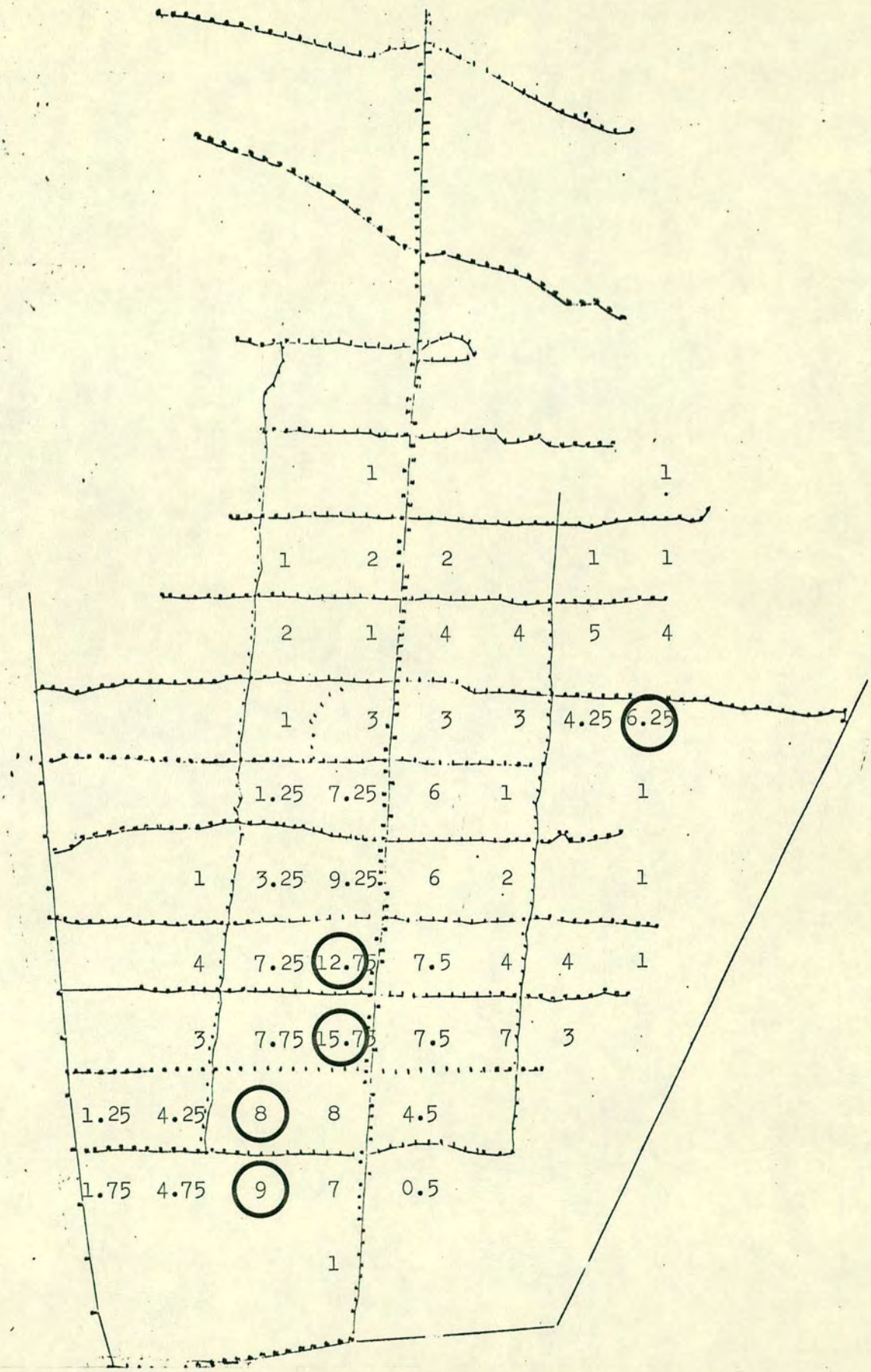
Distribution of raw scores across the intensive study area
BRACHYTELES ARACHNOIDES (only one troop present in the area)



Distribution of raw scores across the intensive study area
CEBUS APELLA : troop "Calmo"
Circles mark the hectares where the scores were particularly high.



Distribution of raw scores across the intensive study area
CEBUS APELLA : troop "Ceva"
Circles mark the hectares where the scores where particularly high.



Distribution of raw scores across the intensive study area
CEBUS APELLA : troop "Porteira"
Circles mark the hectares where scores were particularly high.

APPENDIX II.1
GAZETTEER

Origin of the examined specimens of Cebus apella
(see map at the end)

COUNTRY	LOCALITY CODE	LOCALITY NAME The collector and date of collection (month and year or only year) are in brackets	COORDINATES (Degrees and minutes)	COORDINATES DET. BY (see legend)
BOLIVIA	BOL-1	Chimate (Simons 1900)	15 00S- 68 00W	PN
	BOL-2	Buenavista, Santa Cruz (Steinbach)	17 27S- 63 40W	WK
BRAZIL	-AMAZONAS (AM)			
	AM-1	Eirunepé (=João Pessoa), (including Igarapé Grande), [left bank of R.Juruá]; R.Juruá (Garbe V,XI.1902, Olalla X.1936,I.1937)	06 40S- 69 52W	S
	AM-2	Lagoa Canaçary (or Canaçari) [north bank of R.Amazonas] (Olalla IV.1936,V.1937)	02 58S- 58 15W	S
	AM-3	Itacoatiara (including Lago do Serpa)[north bank of R.Amazonas](Olalla III.1937, IX.1936)	03 07S- 58 28W	S
	AM-4	Igarape Anibá [north bank of R.Amazonas](Olalla 1937, VIII.1936)	02 55S- 58 33W	S
	AM-5	Lago Batista (or Baptista) [south bank of R.Amazonas] (Olalla X.1936; I,V.1937)	03 18S- 58 16W	S
	AM-6	Santa Cruz, R.Eiru, R.Juruá (Olalla X,XI 1936)	07 23S- 70 47W	(PH)
	AM-7	Anajatuba, R.Negro [mispel.Acajatuba,Acajutuba?] (E.Snethlage, VI.1916)	01 33S- 61 35W	S
	AM-13	R.Negro, R.Alegria	01 07S- 64 13W	(WK)
	AM-14	Paraná do Jacaré,Canabouca	03 30S- 60 41W	(PH)
	-AMAPA (AP)			
	AP-1	Vila Velha, Oiapoque (Moreira IV.1952)	03 13N- 51 13W	S
	AP-2	Tracajatuba (Deane III.1969)	01 00N- 51 00W	S
	-ALAGOAS (AL)			
	AL-1	Palmeira dos Índios	09 24S- 36 39W	S
	-BAHIA (BA)			
	BA-1	Rio Gongogi (C.A.Camargo e O.Pinto 1932)	14 28S- 39 50W	S
	BA-2	Vila Nova(=Senhor do Bom Fim) (E.Garbe 1908 or 1915)	10 27S- 40 12W	S
	BA-3	Ilhéus (col. Brandt)	14 45S- 39 02W	S
	BA-4	Itajuí(=Formosa do Rio Preto) [including Faz.Aldeia, Faz. Sucuriú, Faz.Lourenço, Ibipe-		

	tuba](S.E.P.F.A. VIII.1949)	11 03S- 45 10W	S
BA-5	Belmonte [including Passuí] (S.E.P.F.A. VII.1949)	15 51S- 38 54W	S
BA-6	Carinhanha [left bank of R. São Francisco] (S.E.P.F.A. III.1947)	14 18S- 43 48W	S
BA-7	Malhada [right bank of Rio Sao Francisco] (S.E.P.F.A. XI.1947)	14 14S- 43 46W	S
BA-8	Itamaraju	17 03S- 39 30W	S
BA-9	Alcobaça	17 30S- 39 12W	S
BA-10	Prado	17 19S- 39 13W	S
-CEARÁ (CE)			
-CE-1	Bom Jardim(=Potiretama) [Munic.São Benedito] (L.Deane X,XI.1973)	05 43S- 38 09W	S
-ESPÍRITO SANTO (ES)			
ES-1	R. São José (Olalla IX.1942)	19 05S- 40 35W	S
ES-2	Linhares,Res.Florestal Sooretama (L.Deane IV.V.1968)	19 00S- 40 00W	S
ES-3	Vila Colatina(=Colatina) [right bank of R.Doce] (E.Garbe V.1906)	19 32S- 40 37W	S
ES-4	Pau Gigante (E.Garbe V.1906)	19 43S- 40 38W	S
ES-5	Santa Teresa (S.E.P.F.A. - VII.1940)	19 55S- 40 35W	S
ES-6	São Domingos	19 09S- 40 38W	S
ES-7	Engenheiro Reeve (=Rive) (A.Robert IV.1901,III.1903)	20 46S- 41 28W	S
ES-8	Conceição da Barra	18 34S- 39 36W	
-GOIÁS (GO)			
GO-1	Fazenda Santa Adélia, Jataí (E.Dente I.1955)	17 58S- 51 58W	S
GO-2	Ponte do Ipê Arcado (Dreher IV.1904)	18 10S- 47 57W	S
GO-3	R.Araguaia, Faz.Esperança (A.G.Bauer, VII.1906)	15 32S- 49 44W	S
GO-4	Faz.Formiga [right bank of Rio das Almas](J.Lima X.1934)	15 12S- 49 32W	S
GO-5	Inhumas (E.Garbe XI.?1934)	16 20S- 49 31W	S
GO-6	Goiânia (J.Hidasi IX.1963)	16 42S- 49 17W	S
GO-14	Rio dos Pilões	16 12 to 16 20S/ 50 47 to 50 58W	MV
-MARANHÃO (MA)			
MA-1	Miritiba(=Humberto de Campos) (Schwanda X.1906)	02 37S- 43 28W	S
MA-2	Boa Vista (Schwanda X.1906, II,VIII.1907,VIII,XII.1908, I,II.1909, 1910)	02 30S- 43 17W	S
MA-3	Primeira Cruz (Schwanda IX.1906)	02 32S- 43 26W	S
MA-4	Carolina, Faz.Recreio (coll.?, XII.1948)	07 21S- 47 28W	S
MA-5	Santa Luzia (L.Deane X.1969)	04 10S- 46 05W	S
-MINAS GERAIS (MG)			
MG-1	Machacalis (E.Dente XII.1954)	17 04S- 40 45W	S

MG-2	[Vargem] Alegre (B.de Godoy, 1898)	19 35S- 42 18W	S
MG-3	Theophilo Otoni(=Teófilo Otoni)(E.Garbe 1908)	17 52S- 41 29W	S
MG-4	R.Doce,lower Suassuhy(=Suaçuí) [sample includes animals from both banks of R.Doce] (Olalla IX.1940)	18 51S- 41 45W	S
MG-5	Faz.Esperanca, São José da Lagoa (=Nova Era) [on R.Piracicaba] (Olalla X.1940)	19 46S- 43 02W	S
MG-6	Mayrink(=Mairinque) [on R.Macuni,mispel.Mucuri] (E.Garbe XI or II.1908)	17 47S- 40 30W	S
MG-7	R.Matipoo (J.P.Fonseca VII.1919)	19 53S- 42 33W	S
MG-8	Curvelo (S.E.P.F.A. VII.1949) [including Faz.Buenos Aires, Faz.Angical]	18 41S- 44 25W	S
MG-9	Além Paraíba (S.E.P.F.A VIII-1939,I,II.1940,VIII.1943) [including Faz.S.Geraldo, Faz.Paraíso,Faz.Bom Retiro]	21 53S- 42 36W	S
MG-10	Caratinga (L.Deane VII.1971) [including Santo Antonio Manhuaçu]	19 47S- 42 04W	S
MG-11	Matias Barbosa (S.E.P.F.A. - IV,V.1946) [including Faz. Cabui and Mata Grotão]	21 47S- 43 24W	S
MG-13	Araguary(=Araguari) (A.Robert IV,V,VII.1901; S.E.P.F.A. V.1945,IV,VIII. 1946,XII.1943) [including Faz. Piracaíba]	18 39S- 48 12W	S
MG-21	Juiz de Fora	21 45S- 43 23W	S
MG-29	Viçosa	20 45S- 42 49W	S
-MATO GROSSO (MT)			
MT-1	Cuiabá (Pinto 1937; Lima IX.1937)	15 37S- 56 05W	S
MT-2	Coxim,R.Piquery(=Piqueri) (Lima and Lima VII.1930)	17 57S- 54 48W	S
MT-3	Mata do 7 de Setembro [near Porto Garapu, R.Sete de Setembro] (E.Dente e W.Bokermann X.1949)	13 17S- 52 45W	S
MT-4	Chavantina(=Xavantina) (H.Sick I.1947)	Either 21 16S- 52 57W or 14 34S- 51 54W	S
MT-5	Miranda (Lima & Lima VIII, IX.1930)	20 15S- 56 22W	S
MT-6	São Domingos, R. das Mortes (Bokermann, Dente et al, IX & X.1949)	13 28S- 51 25W	S

MT-7	Corumbá (E.Garbe X or XI. 1917; Camargo X.1938)	19 00S- 57 37W	S
MT-8	Salobra [east of R.Paraguai] (Lane VII.1939; Camargo 1940 Lane & Travassos I.1941 [exp. Instituto Oswaldo Cruz]	21 16S- 57 08W	S
MT-9	R.Aricá, Faz.Aricá (A.Aggio VI.1944;Olalla VI.1944 - Exp. Alto Tapajós)	15 42S- 55 53W	S
MT-10	Palmeiras (Olalla V or VI. 1944)	20 27S- 55 30W	S
MT-11	Lagoa Ipavu, Parque Nacional do Xingu (Vanzolini 1965)	12 15S- 53 23W	S
MT-12	Faz.Santa Barbara [right bank of R.Paraná, facing Porto Epitácio] (coll.?, 1962)	21 46S- 52 08W	S
MT-13	Serra da Chapada (A.Robert, VII,VIII,IX,X,XI.1902)	15 26S- 55 45W	PH
-PARÁ (PA)			
PA-1	Foz do Curuá [south bank of R.Amazonas] (Olalla XII.1936)	02 23S- 54 04W	S
PA-2	Bravo(=Igarapé Bravo) [north bank or R.Amazonas] (Olalla V.1935)	02 26S- 55 00W	(PH)
PA-3	Cacoal Grande (mispel.Coral Grande?) [north bank or R. Amazonas] (Garbe 1920)	02 24S- 54 25W	S
PA-4	Faz.Maruá (or Murua, Mararu, Marucu) [south bank of R.Amazonas] (E.Garbe 1920)	02 26S- 54 42W	S
PA-5	Boiuçu(=Boiussu, mispel.Bonissu)[north bank of R.Amazonas] (Olalla IV.1934)	02 26S- 55 00W	S
PA-6	Bom Jardim [south bank of Rio Amazonas] (Olalla III.1936)	01 06S- 50 58W	S
PA-7	Paissandu, Paraná Bom Jardim, Munic. Faro (E.Snethlage II. 1911, M.Amaral & C.T.Carvalho X.1959)	02 11S- 56 44W	(PH)
PA-8	Caxiricatuba [east bank of R.Tapajós] (Olalla I to III. 1937,XII.1937,IV,VI & IX 1935)	02 36S- 54 56W	PH
PA-9	Rio Arapiuns, Aruani [west bank of R.Tapajós] (Olalla V.1936)	02 35S- 55 40W	S
PA-10	Boim [west bank of R.Tapajós) (Olalla XII.1932)	03 01S- 55 14W	S
PA-11	Capim, Rodovia Belém-Brasília km.93 (D.Z.-CNPq IX.1959)	01 40S- 47 45W	S
PA-12	Fordlândia [east bank of Rio Tapajós] (Olalla 1966)	03 40S- 55 30W	PH
PA-13	Urucurituba [west bank of Rio Tapajós] (Olalla 1966)	03 31S- 55 31W	S
PA-14	Barreira [west bank of Rio Tapajós] (Vanzolini XII.1970)	04 04S- 55 45W	S
PA-15	Brasília Legal [west bank of		

	R.Tapajós] (Olalla 1966)	03 49S- 55 35W	S
PA-16	Itupiranga [west bank of Rio Tocantins] (J.Hidasi 1967)	05 09S- 49 22W	S
PA-17	Piquiatuba [east bank of Rio Tapajós] (Olalla XII.1936)	02 40S- 54 58W	(PH)
PA-18	R.Jamanxim (H.Shimada 1976-77)	06 25S- 55 35W	S
PA-24	Igarapé Açu(=Igarapé Assu) (A.Robert I,IV,V.1904)	01 32S- 47 03W	(PH)
PA-25	Taperinha [south bank of Rio Amazonas] (Hagmann 1912,1913, 1914,1915,1916,1917,1918, 1919,1920,1921,1926,1931, 1932,1933,?1939)	02 33S- 54 18W	S
-PARAÍBA (PB)			
PB-1	Mamanguape, Camaratuba (Expedição D.Z. 1957)	06 50S- 35 07W	S
-PERNAMBUCO (PE)			
PE=1	Cariri-Mirim [including Sítio Ferreira Vicente, Sítio Boi] (S.E.P.F.A. X.1949)	07 39S- 39 33W	S
-PARANÁ (PR)			
PR-2	Porto Camargo [east bank of R.Paraná] (Dente & Seraglia I.1954]	23 22S- 53 43W	S
PR-3	Parque Nacional de Iguaçu (L.Deane X.1968)	25 23S- 53 43W	S
PR-4	Porto Natal, Munic.Querencia do Norte [east bank of Rio Paraná] (L.Deane X.1968)	23 05S- 53 28W	S
PR-5	Apucarana [including Jandaia, Mata Pereira, Mata Pradóximo] (S.E.P.F.A. X.1946)	23 34S- 51 27W	S
PR-6	Sertanópolis [including Primeiro de Maio, Sítio São Pedro, Córrego dos Limoeiros] (S.E.P.F.A. VII.1946)	23 02S- 51 02W	S
PR-7	Serra Graciosa [including unidentified local. "Corvo"]	25 15S- 48 49W	S
-RIO DE JANEIRO (RJ)			
RJ-1	Parque Nacional do Itatiaia (Lima VIII.1950; J.G.Silva, 1970)	22 25S- 44 40W	S
RJ-2	Mambucaba (Berla)	23 05S- 44 34W	S
RJ-3	Parati (Ewim)	23 10S- 44 39W	S
-RIO GRANDE DO SUL (RS)			
RS-1	Três Passos [including Santo Augusto, Gleba do Pinhal, Sítio do Engenho] (S.E.P.F.A. VII.1948)	27 33S- 53 56W	S
-SANTA CATARINA (SC)			
SC-1	Colônia Hansa(=Corupa) (Ehrhardt 1901 or 1902, I.1903)	26 25S- 49 16W	S
SC-2	Faz.Rio Turvo,Munic.Garuva (L.Deane X.1964)	26 02S- 48 53W	S
SC-3	Joinville(=Joinvile)		

	(Grossmann 1904; Spetter)	26 17S- 48 50W	S
SC-4	Munic.São Francisco do Sul [including unidentified loc. "Figueira"] (L.Deane VI.1968)	26 15S- 48 41W	S
SC-5	Xapecó [including Faz. Esperança, São Domingos] (S.E.P.F.A. IV.1950)	27 13S- 52 41W	S
SC-6	Ibirama [including Serra do Fachinal, Cia. Hanseática, Alto Dollman] (S.E.P.F.A. - X.1948)	27 03S- 49 33W	S
-SÃO PAULO (SP)			
SP-1	Serra Paranapiacaba (Cypriano VIII.1929)	23 52S- 48 00W	S
SP-2	Belém (Bicego I.1898)	23 33S- 46 33W	S
SP-3	Baurú (E.Garbe 1910)	22 20S- 49 05W	S
SP-4	Itararé (E.Garbe 1903)	24 07S- 49 20W	S
SP-5	Munic.Teodoro Sampaio, Reserva Estadual do Morro do Diabo (Forattini 1957,1958)	22 31S- 52 10W	S
SP-6	Ituverava (E.Garbe 1911)	20 21S- 47 47W	S
SP-7	Barretos (E.Garbe 1904)	20 34S- 48 34W	S
SP-8	Varjão do Guaratuba [right bank] (H.Camargo V.1962)	23 43S- 45 54W	S
SP-9	Serra Cantareira (F.Fonseca & J.Navas IX.1937)	23 22S- 46 36W	S
SP-10	Cananéia (Camargo IX.1934)	25 00S- 47 57W	S
SP-11	Boracéia,Munic.Salesópolis (Travassos Filho VI.1949)	23 40S- 45 50W	S
SP-12	Faz.Barreiro Rico, Município Anhembi (E.Dente II or XI. 1964)	22 39S- 48 09W	S
SP-13	Lins(=Estação Albuquerque Lins)[including Faz.Varjão, Ribeirão Campestre] (Olalla VI.1941)	21 40S- 49 42W	S
SP-14	Ipiranga (A.Dias & E.Dente 1946)	23 34S- 46 37W	S
SP-15	Alto da Serra (E.Garbe III. 1900)	23 47S- 46 19W	(PH)
SP-16	[Ilha] São Sebastião (Gunther II or XI.1907; Bicego IX.1896)	23 48S- 45 19W	S
SP-17	[Munic.] Piedade (E.Dente X.1947)	23 43S- 47 24W	S
SP-18	S.Jerônimo, near Avanhandava (E. Garbe VI.1910)	21 28S- 49 57W	S
SP-19	Itapura [east bank of Rio Paraná] (E.Garbe 1904)	20 38S- 51 31W	S
SP-20	Porto Cabral [east bank of R. Paraná] (Lima & Dente X.1941)	22 20S- 52 38W	S
SP-21	Valparaizo(=Valparaíso) (H.Serapião VII.1931)	21 13S- 50 52W	S
SP-22	Franca (Dreher XII.1902 or I.1903; Garbe 1910 or 1912)	20 33S- 47 23W	S
SP-23	Faz.Santa Madalena, Avaré		

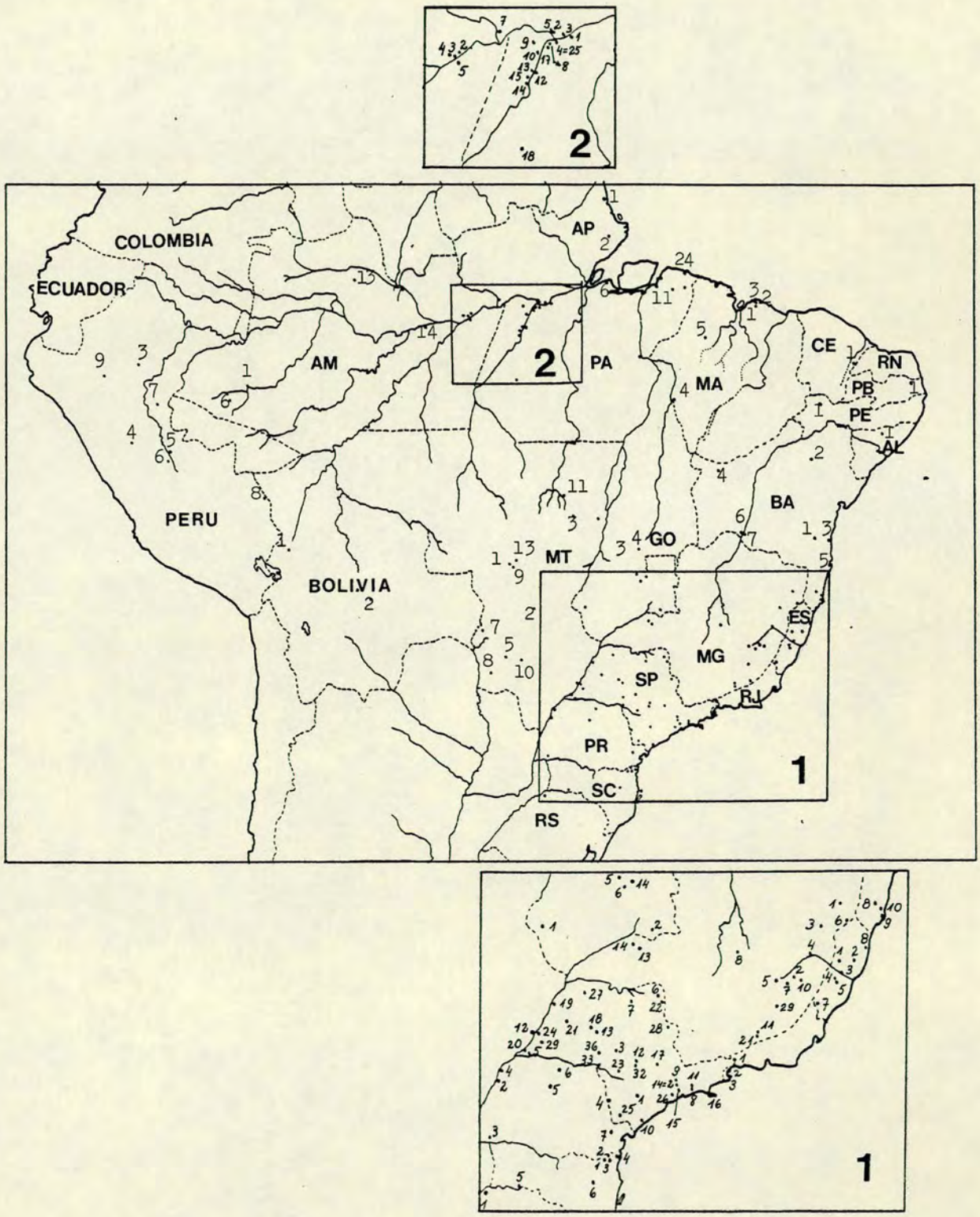
		(Olalla 1963)	23 06S- 48 54W	S
	SP-24	Presidente Epitácio [east bank of Rio Paraná] (J.Lima VII.1926)	21 45S- 52 07W	S
	SP-25	Serra, Munic.Iporanga, plus Lageado, Munic.Iporanga (D.Mota ?1978; C.Lino 1978)	24 36S- 48 45W	S
	SP-26	Estação Engenheiro Ferraz (Olalla 1964)	23 59S- 46 36W	S
	SP-27	Fernandópolis (S.E.P.F.A. - I.1947)	20 10S- 50 16W	S
	SP-28	Mococa (S.E.P.F.A. VII.1946)	21 29S- 47 01W	S
	SP-29	Presidente Venceslau [includ. Faz.Meciaçu, Mata R.Santo Anastácio, Faz.Bandeirantes, Mata da Conserva, Lagoa São Paulo](S.E.P.F.A. XII.1946)	21 57S- 51 51W	S
	SP-32	Victoria (=Vitória de Botucatu) (=Botucatu) (A.Hempel VII.1902)	22 54S- 48 25W	S
	SP-33	Ourinhos (J.Lima III.1901)	23 00S- 49 55W	S
	SP-36	Reserva Estadual "Caitetus" Município Gália	22 24S- 49 39W	S
COLOMBIA				
		Medina	not plotted	
		Villavicencio	not plotted	
ECUADOR				
		(uncertain)		
FRENCH GUYANA				
		Hte. Carsevenne	not plotted	
		Sinnamary, R.	not plotted	
		Ouaqui, R.	not plotted	
		Crique Tamanoir	not plotted	
PERU				
	PERU-1	Santa Ana, Idma, Cuzco	not plotted	
	PERU-2	Huaynapata,Marcapata,Cuzco (Kalinowski VII.1897)	unidentifiable locality	PV
	PERU-3	Chamicuros, Huallaga	05 10S- 75 30W	PH
	PERU-4	Tingo Maria, Huanuco	09 08S- 75 57W	PH
	PERU-5	Cumaria(=Cumeria) (R.W.Hendee col.)	09 52S- 74 01W	PH
	PERU-6	Chicosa, upper Ucayali, Loreto	10 21S- 74 00W	PH
	PERU-7	Cerro Azul, Contamana, Loreto	07 14S- 74 34W	PH
	PERU-8	R.Tahuamanu	12 20S- 68 45W	PN
	PERU-9	Yurac Yacu, San Martin	05 52S- 77 14W	PH

Legend:
PN- coordinates from Napier 1976
PH- coordinates from Hershkovitz 1977
WK- coordinates from Kinzey 1980

PV- Vanzolini, pers. commun.
MV- Vivo, pers.commun.
S - coordinates were relocated during this study, using information from various sources (see Methods in Chapter 4)
()- the coordinates were copied from the indicated source between brackets because my re-location had yielded less precise coordinates
Abbreviations:
S.E.P.F.A.- (for "Servico de Estudos e Pesquisas sobre Febre Amarela") = Yellow Fever Research Service
R.- (for "Rio") = river
Faz. - (for "Fazenda") = farm
Munic. - (for "Município") = county
Res. - (for "Reserva") = florestal reserve

Obs.: When the collector is missing, either the information is not available or the material from that locality was only superficially examined.

Fig. App.II.1 - The countries and (in Brazil) the States from where I examined specimens. For the Brazilian States only codes are given - the full State names are given in the text of Appendix II.1. The numbers are the localities where the specimens where collected; within each State the numbering starts from one.



APPENDIX II.2
SPECIMENS EXAMINED

Code:
BM - British Museum (Natural History); London, Great Britain
HN - Museum National d'Histoire Naturelle; Paris, France
SP - Museu de Zoologia da Universidade de São Paulo; São Paulo, Brazil
MG - Museu Paraense Emílio Goeldi; Belém, Brazil
MN - Museu Nacional; Rio de Janeiro, Brazil
PI - Museu do Parque Nacional de Itatiaia; Itatiaia, Brazil

Type specimens are identified by the form name in brackets after the museum number.

LOCALITY [see app.II.1 for details]	S P E C I M E N S N U M B E R S [S.N.= specimen waiting to be included in the collection] [( ) = field number]
"South America"	HN 595 (holotype of crassiceps Pucheran 1857 acc.Rode 1938) /HN 596 (holotype of hypomelas Pucheran 1857 acc.Rode 1938) /HN 589 (probably the holotype of frontatus [separated by Kuhl after 1820], and not a paralectotype as indicated by Rode 1938)/ HN 588 (probably a paratype of frontatus [separated by Kuhl after 1820] and not the holotype as indicated by Rode 1938)
"Bolivia"	BM 1847.11.22.3 (type of pallidus Gray 1865, acc.Napier 1976)
Bolivia	
-Chimate	BM 1901.2.1.1 (type of sagitta Pusch 1941 - a lectotype, according to Napier 1976)
-Buenavista	BM 26.12.4.2/ BM 26.12.4.4/ BM 34.9.2.3./BM 26.12.4.3/... BM 26.12.4.5/ BM 28.2.9.4
French Guyana	11 specimens at HN. Numbers not copied
Peru	
-Santa Ana	3 specimens at BM. Numbers not copied
-Marcapata	BM 1900.11.5.2 (holotype of peruanus Thomas 1901), and one more specimen at BM, number not copied
-Chamicuros	1 specimen at BM. Number not copied
-Tingo Maria	2 specimens at BM. Numbers not copied
-Cumeria	BM 28.5.2.8./ BM 28.5.2.13/ BM 28.5.2.15/ BM 28.5.2.14
-Chicosa	Specimens at BM. Numbers not copied
-Cerro Azul	2 specimens at BM. Numbers not copied
-Tahuamanu	1 specimen at BM. Number not copied
-Yurac Yaco	3 specimens at BM. Numbers not copied
"Brasil"	HN 570 (holotype of variegatus Geoffroy 1812, acc.Rode 1938) /HN 584 (holotype of cirrifer Geoffroy 1812, acc.Rode 1938) BM 1861.5.26.1 (holotype of leucogenys Gray 1865, acc.Napier 1976)

Brasil

-AL-1	SP 9999
-AM-1	SP 6261/ BM 3.9.1.4./ SP 923/ SP 779/ SP 5135/ SP B.922/ SP 778
-AM-2+3+4	SP 10554/ SP 10549/ SP 5467/ SP 10561/ SP 5125/ SP 10502/ SP 10550
-AM-5	SP 5389/ SP 10545/ SP 5391/ SP10501/ SP 4811/ SP 5569/ SP 10498/ SP 7148/ SP 10553/ SP 10543/ SP 10548/ SP 10543/ SP 10500/ SP 10497/ SP 5390/ SP 5388/ SP 5386/ SP 5385/ SP 5392/ SP 10547/ SP 10558/ SP 5044/ SP 10539/ SP 10552/ SP 5670/ SP 10553/ SP 10557/ SP 10556/ SP 5387
-AM-6	SP 5315/ SP 5192/ SP 5316/ SP 5856/ SP 5321/ SP 5314/ SP 5319/ SP 5317/ SP 5318/ SP 5746/ SP 5320/ SP 5322/ SP 5376 or 5393
-AM-7	BM 1920.7.14.2
-AP-1	SP 9959
-AP-2	SP S.N.(1339)/ SP S.N.(1340)
-BA-1	SP 3860/ SP 3858/ SP 3859/ SP 3848/ SP 3849/ SP 3851/ SP 3850
-BA-2	SP 2583/ SP 2582/ SP 2586/ SP 2585/ SP 2584/ SP 2587
-BA-3	BM 43.6.6.6.x/ BM 1845.6.17.2/ BM 42.6.6.6
-BA-4	MN 23238/ MN 23246/ MN 23236/ MN 23244/ MN 23235/ MN 23247/ MN 23240/ MN 23243/ MN 23245/ MN 23250/ MN 23249
-BA-5	MN 23229/ MN 23228/ MN 23233/ MN 23234/ MN 23232/ MN 23230
-BA-6	MN 23237
-BA-7	MN 23231
-CE-1	MN 23327 or 659
-ES1+6	SP 6201/ SP 6200, plus several specimens at MN (numbers not noted)
-ES-2	SP 11172/ SP 11188/ SP 11170/ SP 11168/ SP 11171/ SP 11167/ SP 11169/ SP 11174/ SP 11175/ SP 11178/ SP 11179/ SP 11166/ SP 11176/ SP 11189/ SP 11162/ SP 11177/ SP 11165/ SP 11187/ SP 11163/ SP 11173
-ES-3	SP 2218/ SP 2213/ SP 2217/ SP 2214/ SP 2216
-ES4+5	SP 2215/ MN 3897
-ES7	BM 1903.9.4.20/ BM 1903.9.4.18/ BM 1903.9.4.19
-GO-1	SP 7907/ SP 7905/ SP 7906
-GO-2	SP 1430
-GO-3	SP 2365/ SP 2364
-GO-4	SP 3948
-GO-5	SP 3937
-GO-6	SP 10642/ SP S.N.(3)/ SP S.N.(16)
-GO-14	HN 580(447) (holotype of elegans Geoffroy 1850,acc.Rode 1938)
-MA1+2+3	SP 2493/ SP 2382/ SP 2741/ SP 2577/ BM 12.7.26.1/ SP 2741/ SP 2742/ SP 2744/ SP 2883/ SP 2743/ SP 2488/ SP 2885/ SP 2888/ SP 2887/ SP 2746/ MG 10/ SP 2386/ SP 2381/ SP 2882/ SP 2886/ SP 2745/ SP 2884
-MA-4	MN 23322/ MN 23323
-MA-5	MN 23324
-MG-1	SP 7879/ SP 7880
-MG-2	SP 294
-MG-3	SP 2717/ SP 2718/ SP 2719/ SP 2715/ SP 2720
-MG-4	SP 5916/ SP 5915/ SP 5917/ SP 5914/ SP 5920/ SP 5919/ SP 5918
-MG-5	SP 5921
-MG-6	SP 2716/ SP 2716-1
-MG-7	SP 3532
-MG-8	MN 23453/ MN 23452
-MG-9	MN 7622/ MN 3895/ MN 3900/ MN 7629/ MN 3899/ MN 7633
-MG-10	MN 23454/ MN 23455

-MG-11	Specimens at MN (numbers not noted) plus MN 23366/ MN 23377/ MN 23378/ MN 23379/ MN 23376/ MN 23367/ MN 23368/ MN 23375/ MN 23365
-MG13+14	MN 23295/ MN 23291/ MN 23292/ MN 23287/ MN 23284/ MN 23288/ BM 1901.11.3.4 (holotype of versuta Elliot 1910, acc.Napier 1976) / BM 1.11.3.1/ BM 1.11.3.3/ BM 1.11.3.5/ MN 23289/ MN 7640/ MN 23281/ MN 23282
-MT1+9+13	Specimens at BM (numbers not noted) plus SP 6319/ BM 3.7.7.6/ BM 3.7.7.178/ BM 3.7.7.1/ BM 3.7.7.8/ BM 3.7.7.2/ BM 3.7.7.5/ BM 1903.7.7.9/ SP 6321/ SP 6325/ SP 6320/ BM 3.4.4.12/ BM 3.7.7.11/ BM 3.7.7.10/ SP 6322/ BM 3.7.7.13/ SP 6317/ SP 6318/SP 4262/ SP 4262x
-MT-2	SP 3770/ SP 3772/ SP 3771
-MT-3	SP 6961/ SP 6966
-MT-4	SP 6713
-MT-5	SP 3775/ SP 3773/ SP 3776/ SP 3772/ SP 3774
-MT-6	SP 6969/ SP 6970/ SP 6960/ SP 6964/ SP 6963/ SP 6971/ SP 7040/ SP 6972/ SP 6965/ SP 6967
-MT-7	SP 3360/ SP 3363/ SP 3361/ SP 4317/ SP 3362
-MT-8	SP 4299/ SP 4300/ SP 5895/ SP 5893/ SP 5894/ SP 5788
-MT-10	SP 6323/ SP 6324
-MT-11	SP 10716
-MT-12	SP S.N.(S.N.)
-PA-1	SP 10536/ SP 5129/ SP 10499/ SP 10544/ SP 10538/ SP 5130/ SP 5464/ SP 5127/ SP 5466/ SP 5131
-PA2+5	SP 10546/ SP 5115/ SP 5134/ SP 5116/ SP 5117/ SP 5126/ SP 5114
-PA-3	SP 3636
-PA4+25	SP 3633/ SP 3634/ MG 4682/ MG 5715/ MG 5085/ MG 5695/ MG 5055/ MG 5077/ MG 5692/ MG 4984/ MG 5689/ MG 5069/ MG 5080/ MG 5073/ MG 4930/ MG 4954/ MG 5086/ MG 4969/ MG 4929/ MG 5054/ MG 4994/ MG 4702/ MG 5711/ MG 5084/ MG 4699/ MG 4990/ MG 5064/ MG 4910/ MG 5076/ MG 4919/ MG 5066/ MG 5701/ MG 5052/ MG 5081/ MG 5693/ MG 5068/ MG 5065/ MG 5074/ MG 5082/ MG 5705/ MG 5053/ MG 4946/ MG 5057/ MG 5697/ MG 4926/ MG 5698/ MG 4920/ MG 4945/ MG 4684/ MG 5005/ MG 4995/ MG 4927/ MG 4986/ MG 4692/ MG 4944/ MG 4911/ MG 4989/ MG 4972/ MG 4988/ MG 4928/ MG 4698/ MG 4933/ MG 4950/ MG 5072
-PA-6	SP 5128/ SP 5132
-PA-7	BM 12.5.11.3/ SP 8956/ SP 8957/ SP 8959/ SP 8958
-PA8+17	SP 10537/ SP 5753/ SP 10541/ SP 5120/ SP 5121/ SP 5752/ SP 10540/ SP 5118/ SP 10535/ SP 10503/ SP 5123/ SP 5024 or 5124/ SP 5122/ SP 5119
-PA9+10	SP 4291/ SP 5674/ SP 5675
-PA-11	SP 8920
-PA-12	SP S.N.(1958)/ SP S.N.(806)/ SP S.N.(934)/ SP S.N.(2176)/ SP S.N.(2174)/ SP S.N.(1103)/ SP S.N.(2026)/ SP S.N.(936)/ SP S.N.(1956)/ SP S.N.(2173)/ SP S.N.(2175)/ SP S.N.(2177)/ SP S.N.(917)/ SP S.N.(1018)/ SP S.N.(1951)/ SP S.N.(1950)/ SP S.N.(2169)/ SP S.N.(2171)/ SP S.N.(1952)/ SP S.N.(973)/ SP S.N.(1947)/ SP S.N.(914)/ SP S.N.(2034)/ SP S.N.(2172)/ SP S.N.(2170)/ SP S.N.(950)/ SP S.N.(1955)/ SP S.N.(1953)/ SP S.N.(1954)/ SP S.N.(1823)/ SP S.N.(14)/ SP S.N.(15)/ SP S.N.(11)
-PA-13	SP S.N.(1825)/ SP S.N.(1959)/ SP S.N.(235)/ SP S.N.(2023)/ SP S.N.(2022)/ SP S.N.(1948)/ SP S.N.(712)/ SP S.N.(233)/

	SP S.N.(2020)/ SP S.N.(2027)/ SP S.N.(951)/ SP S.N.(29)/ SP S.N.(27)/ SP S.N.(1960)/ SP S.N.(2025)/ SP S.N.(2024)/ SP S.N.(2021)
-PA-14	SP S.N.(1947)
-PA-15	SP S.N.(70.1495)
-PA-16	SP S.N.(4)
-PA-18	One specimen from a private collection
-PA-24	BM 4.7.4.15/ BM 4.7.4.16/ BM 4.7.4.12/ BM 4.7.4.13/ BM 4.7.4.14
-PB-1	SP 8450
-PE-1	MN 23316/ MN 23313/ MN 23314/ MN 23320/ MN 23321 or 23322/ MN 23317/ MN 23310/ MN 23309
-PR2+4	SP S.N.(19)/ SP S.N.(24)/ SP 7710/ SP S.N.(17)/ SP S.N.(26)
-PR-3	SP S.N.(22)/ SP S.N.(21)
-PR-5	MN 23490/ MN 23493/ MN 23492/ MN 23489/ MN 23491
-PR-6	MN 23488/ MN23500/ MN 23501/ MN 23498/ MN 23497/ MN 23487
-PR-7	MN 2977 or 922
-RJ-1	SP 7056/ SP 7055/ SP 9424/ MN 21171/ PI 1467/ PI 1466
-RJ-2	MN 8516/ MN 8341
-RJ2 or 3	MN 23364
-"Rio Grande do Sul"	BM 1893.1.1.11
-RS-1	MN S.N.(M29242)/ MN S.N.(M29214)/ MN S.N.(M29203)/ MN S.N.(M29210)/ MN S.N.(M29235)/ MN S.N.(M29207)/ MN S.N.(M29223)/ MN S.N.(M29218)/ MN S.N.(M29220)/ MN S.N.(M29209)/ MN 23517/ MN 23519/ MN S.N.(M29202)/ MN S.N.(M29243)/ MN S.N.(M29230)/ MN S.N.(M29200)/ MN S.N.(M29215)/ MN S.N.(M29206)/ MN S.N.(M29212)/ MN 23521/ MN S.N.(M29217)/ MN S.N.(M29225)/ MN S.N.(M29221)/ MN 23518/ MN S.N.(M29228)/ MN S.N.(M29246)/ MN S.N.(M29204)/ MN S.N.(M29239)/ MN 23520/ MN S.N.(M29244)/ MN S.N.(M29229)/ MN S.N.(M29241)/ MN S.N.(M29202)A
-SC1+2+3	SP 7133/ BM 1903.9.1.15 (holotype of caliginosus Elliot 1910, acc. Napier 1976)/ SP 432/ SP 1667/ SP 884/ BM 22.5.29.2/ BM 1922.5.9.1/ SP 431/ SP 868/ SP 434
-SC-4	SP S.N.(994)/ SP S.N.(998)/ SP S.N.(995)/ SP S.N.(993)/ SP S.N.(996)/ SP S.N.(992)
-SC-5	MN 23516/ MN 23515
-SC-6	MN 23514/ MN 23513/ MN 23511/ MN 23512/ MN S.N.(M29282)/ MN S.N.(M29249)/ MN S.N.(M29275)/ MN S.N.(M29278)/ MN S.N.(M29274)/ MN S.N.(M29247)/ MN S.N.(M29250)/ MN S.N.(M29292)/ MN S.N.(M29258)/ MN S.N.(M29284)/ MN S.N.(M29245)/ MN S.N.(M29297)/ MN S.N.(M29293)/ MN S.N.(S.N.)/ MN S.N.(M29283)/ MN S.N.(M29252)/ MN S.N.(M29295)/ MN S.N.(M29276)
-"São Paulo"	NH 585 (holotype of vellerosus Geoffroy 1851,acc.Rode 1938)/ NH 586 (paratype of vellerosus Geoffroy 1851,acc.Rode 1938)
-SP-1	SP 3813
-SP2(=14)+9	SP 6483/ SP 2440/ SP 6638
-SP-3	SP 466/ SP 459/ SP 2858/ SP 491/ SP 490/ SP 489
-SP-4	SP 1157/ SP 1158/ SP 1155/ SP 1156
-SP-5	SP 8493/ SP 8905
-SP6+22	SP 816/ SP 830A/ SP 833/ SP 2926/ SP 829/ SP 3007/ BM 3.9.1.14/ SP 828/ BM 3.9.1.16/ SP 794/ SP 830/ SP 790/ SP 815/ SP 832/ SP 2925/ SP 831/ SP 3003/ SP 3005/ SP 3004/ SP 3006
-SP7	SP-1418
-SP8=11	SP 6887/ SP 9641/ SP 9642/ SP 9640

-SP-10	SP 3909
-SP12+32	BM 1903.7.25.1/ SP 10342/ SP 10343/ SP 10341/ SP 10349/ BM 1903.7.25.2, and observations on wild animals.
-SP13+18	SP 5902/ SP 5906/ SP 3151A/ SP 3152A/ SP 2859/ SP 2855/ SP 2852/ SP 2857/ SP 2863/ SP 3151/ SP 6165/ SP 5903/ SP 2849/ SP 5905/ SP 2850/ SP 2864/ SP 2859A/ SP 2853/ SP 2856/ SP 5904/ SP 2860/ SP 2854/ SP 3152/ SP 5907
-SP-15	SP 397/ SP 400/ SP 398
-SP-16	SP 98/ SP 2548
-SP-17	SP 6733
-SP-19	SP 1934
-SP-20	SP 6013/ SP 6014/ SP 6015/ SP 6016/ SP 6017
-SP-21	SP 3812/ SP 3815
-SP-23	SP 10327
-SP-24	SP 3715/ SP S.N.(S.N.)/ SP S.N.(CTA-3)/ SP S.N.(CTA-2)
-SP-26	SP S.N.(1248)/ SP S.N.(1249)/ SP S.N.(1250)
-SP-27	MN 23475/ MN 23473/ MN 23461/ MN 23465/ MN 23470/ MN23468/ MN 23456/ MN 23471/ MN 23469/ MN 23467/ MN 23474/ MN23476/ MN 23462/ MN 23463/ MN 23457/ MN 23460/ MN 23466
-SP-28	MN 23482/ MN 23486/ MN 23485/ MN 23483/ MN 23484
-SP-29	MN 23477/ MN 23479/ MN 23478/ MN 23481/ MN 23480
-SP-33	SP 421, and observations on wild animals.
-SP-34	SP 2851
-SP-35	SP 6586
-SP-36	Observations on wild animals.

APPENDIX II.3
SEXUAL DIMORPHISM IN THE MORPHOMETRIC CHARACTERS

For each case (i.e. each combination of locality and sex), three numbers are given: the one between brackets is the mean character value; the ones to the left and to the right of the brackets are respectively the smallest and the largest values. A "*" indicates that there is significant difference ($p<0.05$) between the male and the female means. Two asterisks indicate that there is no overlap between the male and the female ranges.
All localities with at least 4 adult skulls of each sex are included. The ranges and means in this table come from the raw data, i.e., measurements were not standardized to age 12.
(M) - males; (F) - females

LOCALITY		CHARACTERS		
		G1	H1	I1
PA12	M	94.1 (97.8) 103.0*	71.6 (78.0) 83.7*	48.9 (52.0) 55.0
	F	88.0 (91.5) 94.8	67.0 (70.5) 75.4	48.6 (51.0) 55.2
PA13	M	93.6 (97.0) 100.3*	72.2 (76.0) 79.6*	48.6 (51.9) 54.9
	F	83.2 (87.5) 93.8	65.1 (67.9) 72.2	48.1 (49.2) 50.5
AM6	M	99.9(102.8) 105.8*	79.6 (83.6) 85.5**	50.0 (52.0) 54.5
	F	95.0 (97.4) 100.4	73.6 (75.6) 77.4	50.9 (51.7) 53.5
AM5	M	96.2 (98.4) 102.5**	75.0 (78.4) 81.1**	48.7 (52.4) 54.5*
	F	85.0 (90.4) 94.6	65.0 (69.0) 72.7	48.5 (50.4) 53.2
SC1	M	101.5(103.8) 106.0**	74.4 (80.9) 86.0*	49.8 (53.1) 56.5
	F	95.0 (96.8) 99.4	70.5 (73.5) 76.4	50.0 (52.1) 53.5
SC6	M	100.5(103.2) 104.2**	80.7 (81.6) 82.4**	53.5 (54.5) 56.1*
	F	92.8 (94.6) 96.5	69.3 (71.3) 74.5	50.1 (51.6) 54.6
RS1	M	99.5(102.1) 103.9**	77.7 (76.8) 82.5**	51.5 (52.9) 53.6*
	F	89.8 (92.9) 97.2	68.1 (70.6) 75.6	48.0 (50.8) 52.7
SP13	M	92.0 (98.1) 101.0*	72.5 (77.1) 80.8*	50.0 (52.8) 54.9*
	F	90.0 (94.3) 99.8	68.0 (70.7) 74.1	48.9 (51.1) 53.3
SP27	M	92.0 (95.6) 99.5*	69.0 (74.7) 79.2*	49.5 (51.8) 53.8
	F	88.5 (92.1) 95.8	65.4 (69.7) 74.0	50.0 (51.2) 52.5
ES2	M	98.2(100.2) 103.0**	77.7 (79.1) 80.6**	50.6 (51.6) 53.0
	F	90.8 (94.4) 96.9	70.1 (73.6) 77.0	47.7 (49.8) 51.0
MG13	M	91.5 (97.4) 101.3**	72.3 (76.7) 80.8**	47.3 (51.8) 53.8
	F	87.6 (89.3) 90.5	68.0 (69.0) 70.6	47.7 (50.4) 52.7
MG11	M	95.5(101.0) 105.9**	73.8 (78.1) 84.3**	48.5 (50.0) 53.1
	F	90.8 (92.2) 94.3	69.8 (71.0) 72.0	47.0 (48.1) 49.4
MA1	M	93.0 (97.7) 103.5**	70.4 (76.8) 82.0**	48.4 (50.7) 52.5
	F	85.1 (88.1) 90.3	65.5 (67.4) 70.0	49.6 (50.2) 51.7
PA25	M	90.9 (97.9) 103.9*	73.5 (78.5) 83.0**	48.8 (52.1) 54.9**
	F	85.9 (89.8) 93.7	64.4 (69.0) 73.4	48.5 (50.7) 54.2
MT13	M	93.7 (98.8) 102.6*	74.9 (78.0) 81.6*	49.5 (51.6) 53.8
	F	88.8 (91.5) 98.5	67.8 (70.1) 75.1	48.7 (50.0) 51.5

LOCALITY		CHARACTERS J1	CHARACTERS K1	CHARACTERS L1
PA12	M	64.5 (71.0) 75.7**	48.1 (54.4) 58.7*	35.5 (41.9) 46.5*
	F	59.2 (60.4) 62.7	47.5 (49.9) 53.5	33.8 (36.3) 38.6
PA13	M	62.9 (67.2) 73.5**	49.5 (51.5) 54.0*	39.4 (40.1) 33.4**
	F	54.8 (56.4) 58.5	43.7 (46.5) 50.8	30.9 (33.4) 36.9
AM6	M	69.1 (74.3) 78.3**	54.8 (56.6) 58.2*	40.9 (45.6) 47.5*
	F	63.5 (64.9) 68.0	51.8 (53.3) 55.7	39.2 (40.9) 42.5
AM5	M	66.2 (69.8) 73.8**	49.0 (52.6) 56.3**	38.5 (41.1) 45.0*
	F	56.3 (59.0) 63.3	45.8 (48.0) 52.0	32.8 (35.0) 39.0
SC1	M	63.1 (70.0) 75.5*	49.5 (54.0) 58.2*	34.5 (42.1) 46.2
	F	58.5 (62.1) 65.1	46.9 (49.0) 52.0	32.0 (36.9) 40.4
SC6	M	70.6 (73.6) 76.0**	50.5 (53.6) 56.3*	35.6 (41.5) 46.9*
	F	59.4 (61.2) 63.5	46.4 (47.7) 49.5	33.7 (35.2) 37.1
RS1	M	67.7 (69.1) 70.8**	50.4 (52.4) 54.2**	40.8 (42.4) 44.6**
	F	58.0 (59.8) 62.6	45.8 (47.3) 50.2	32.0 (34.9) 37.9
SP13	M	59.8 (67.0) 73.0*	46.4 (51.5) 57.0*	34.2 (40.1) 47.7*
	F	58.0 (60.2) 62.7	45.7 (48.7) 51.4	34.4 (36.7) 40.0
SP27	M	57.3 (64.3) 69.0*	45.9 (50.3) 53.1*	32.1 (37.7) 43.2
	F	56.9 (59.9) 63.1	44.3 (47.3) 51.1	31.5 (34.8) 37.6
ES2	M	69.5 (72.7) 75.4**	52.8 (54.8) 56.3**	40.2 (43.1) 45.2**
	F	59.9 (61.5) 63.4	46.0 (48.8) 50.4	37.0 (38.1) 39.0
MG13	M	60.8 (68.7) 72.9**	47.4 (52.5) 55.7*	37.1 (42.0) 47.2*
	F	58.4 (59.3) 60.2	46.6 (47.5) 48.0	33.8 (36.0) 38.4
MG11	M	64.9 (70.2) 73.4**	50.0 (52.0) 53.7**	42.0 (45.3) 48.8**
	F	59.2 (61.4) 62.3	47.9 (48.7) 49.5	39.0 (40.0) 41.5
MA1	M	60.3 (68.2) 77.0*	48.5 (52.0) 55.6**	36.4 (43.5) 48.9*
	F	57.8 (59.0) 60.7	45.5 (47.1) 47.9	36.4 (37.6) 39.4
PA25	M	60.1 (69.0) 76.5*	49.6 (53.6) 58.2*	35.1 (40.9) 47.5*
	F	55.5 (58.4) 62.0	45.3 (48.4) 51.5	29.5 (33.7) 38.1
MT13	M	65.0 (70.7) 74.2**	50.6 (53.2) 56.0*	37.3 (40.2) 42.9**
	F	56.0 (58.7) 60.3	48.8 (49.8) 51.7	32.2 (34.6) 37.2

LOCALITY		CHARACTERS N1	A2	C2	D2
PA12	M	14.5 (16.1) 18.2**	740 (843) 930*	350 (425) 464	105 (122) 140*
	F	9.9 (10.9) 12.0	700 (795) 870	390 (419) 465	98 (110) 120
PA13	M	15.1 (15.9) 16.7**	790 (860) 920	350 (423) 460	98 (obs) 120
	F	9.2 (10.4) 11.2	750 (771) 810	350 (378) 395	100 (obs) 110
AM6	M	17.4 (18.6) 19.5**	---	---	---
	F	11.4 (11.4) 11.5	---	---	---
AM5	M	15.9 (17.1) 18.5**	---	---	---
	F	10.0 (10.7) 11.5	---	---	---
SC1	M	16.4 (17.2) 18.1**	---	---	---
	F	10.2 (10.7) 11.9	---	---	---
SC6	M	10.6 (14.2) 16.0*	---	---	---
	F	8.8 (9.8) 11.0	---	---	---
RS1	M	14.5 (16.2) 17.1**	---	---	---
	F	8.5 (9.8) 11.0	---	---	---
SP13	M	15.0 (16.1) 17.8**	---	---	---
	F	9.8 (11.1) 12.1	---	---	---
SP27	M	15.0 (17.3) 18.0**	740 (800) 860	390 (417) 450*	118 (122) 130*
	F	10.3 (11.0) 12.0	730 (762) 805	380 (397) 425	113 (116) 120
ES2	M	16.0 (17.2) 18.0**	---	---	---
	F	10.1 (10.6) 11.0	---	---	---
MG13	M	15.3 (16.5) 17.6**	830 (865) 890*	440 (458) 470	125 (129) 138**
	F	10.1 (10.8) 11.7	780 (810) 847	426 (443) 468	107 (112) 121
MG11	M	14.0 (16.0) 18.8**	820 (861) 890	430 (438) 447	121 (129) 136*
	F	9.5 (10.4) 11.3	800 (850) 890	415 (443) 475	111 (119) 125
MA1	M	14.9 (16.1) 18.5**	---	---	---
	F	9.3 (10.3) 11.0	---	---	---
PA25	M	14.7 (16.8) 19.3**	---	---	---
	F	9.5 (10.4) 12.4	---	---	---
MT13	M	14.8 (16.0) 16.7**	820 (876) 940*	385 (424) 450	111 (117) 125*
	F	10.3 (10.8) 11.1	760 (791) 837	360 (400) 427	102 (108) 112
MT6	M	---	790 (867) 950	390 (414) 445	110 (114) 120
	F	---	680 (801) 850	310 (364) 410	98 (108) 113

(obs.)= difference between means not tested (sample too small)

APPENDIX II.4

Means, standard deviations (for M1, range instead of st.dev.) and sample sizes for the skull characters in each major locality. Characters G1,H1,J1,K1 of males and characters J1,K1,L1,N1 of females have been standardized to age category 12. Note that each sample had at least 4 specimens but due to skull damage, some measurements are missing and the final sample size is sometimes smaller than 4. For M1 the sample size is two times the number of specimens because the pneumatization is independent in each of the two vomer wings.

Obs.- The standard deviation is proportional to the mean value of the variable and therefore is not the best indication of variability, which is best represented by the coefficient of variation (C.V.= st.dev./mean). After standardization for age 13, the C.V.s are around 5%. Before standardization, they were often beyond 10% (particularly for J1,L1 and K1, which are strongly affected by age). The standardization does not artificially lower the variability - it simply reveals what the variation really is for a given age.

MALES

LOCALITY	G1	H1	I1	J1	K1	L1	N1	M1
AM1	104.6	84.9	54.6	77.0	58.5	47.0	18.6	2.7
	2.6	2.2	1.5	3.2	2.6	2.0	1.3	(2-3)
	4	4	4	4	4	4	3	8
AM2	99.3	78.9	51.8	70.0	53.6	42.5	16.9	2.8
	2.9	3.3	0.2	4.1	1.4	2.1	0.8	(2-3)
	5	5	5	5	5	5	5	10
AM5	98.6	79.1	52.4	70.1	52.9	41.5	17.4	2.8
	2.3	2.4	1.8	2.3	2.4	2.1	0.8	(2-3)
	11	11	11	11	11	11	11	22
AM6	102.0	83.7	52.0	73.5	56.4	45.3	18.7	2.3
	2.2	2.3	1.6	2.7	0.8	2.1	0.7	(1-3)
	6	6	6	6	5	6	6	12
BOL2	101.9	80.8	53.0	70.4	54.1	43.6	16.9	2.6
	2.8	3.5	1.7	4.2	3.1	5.4	0.0	(2-3)
	4	4	4	4	4	4	2	4
ES2	99.5	79.6	51.6	72.4	54.7	43.0	17.3	2.2
	1.0	0.7	1.1	3.2	1.2	1.3	1.1	(1-3)
	4	3	4	4	4	4	3	8
MA1	97.9	77.7	50.7	68.9	52.4	44.3	16.4	2.2
	2.9	2.8	1.2	3.7	2.0	3.1	1.2	(1-3)
	13	13	13	12	13	13	11	20
MG11	100.4	78.6	50.0	70.2	52.1	45.7	16.3	1.8
	2.1	2.7	1.8	1.6	0.9	2.0	1.5	(1-3)
	5	5	5	5	5	5	5	6
MG13	98.6	78.4	51.8	70.7	53.3	43.5	17.3	2.1
	3.4	2.8	2.1	4.6	3.1	3.1	1.3	(1-3)
	8	8	8	8	8	8	6	16
MG4	99.3	79.4	51.6	68.5	53.0	39.9	18.0	2.3
	0.8	1.4	0.6	0.9	1.4	0.6	1.9	(1-3)
	4	4	4	3	4	4	4	8

MT6	95.0	73.4	48.3	67.2	51.4	41.4	16.1	2.3
	2.2	1.4	0.7	3.0	2.5	3.7	0.7	(1-3)
	3	3	4	4	2	4	3	8
MT13	98.5	78.9	51.6	71.3	53.6	41.1	16.7	2.8
	4.4	3.3	1.7	4.3	2.1	2.5	0.7	(2.5-3)
	7	7	6	7	7	7	6	12
PA12	97.9	78.9	52.0	71.9	54.8	42.4	16.5	2.3
	3.0	3.2	1.6	2.6	2.9	3.1	1.0	(1-3)
	13	13	13	11	13	13	12	24
PA13	98.0	77.8	51.9	68.9	52.2	41.2	16.5	2.9
	2.5	2.9	2.4	4.1	1.8	0.8	0.6	(2-3)
	5	5	5	4	5	5	5	8
PA25	97.8	79.3	52.1	69.4	53.9	41.3	17.0	2.6
	2.8	2.6	1.3	3.8	2.3	2.9	1.2	(1-3)
	30	30	31	29	31	31	27	58
PA8+	99.9	81.1	53.2	73.4	54.6	43.9	17.9	2.9
	1.4	2.2	1.1	2.2	1.7	1.8	1.5	(2-3)
	7	7	7	7	7	7	6	14
RS1	103.7	82.3	52.9	72.3	54.0	45.0	16.9	1.5
	2.4	1.9	0.8	2.8	0.6	1.9	1.0	(1-3)
	5	5	5	5	5	5	5	6
SC1+	104.0	82.0	53.1	70.9	54.8	43.1	---	2.3
	1.3	2.6	2.4	2.7	1.6	3.2	---	(2-3)
	6	6	6	6	6	6	0	12
SC6	105.0	83.8	54.5	75.0	55.2	44.5	16.0	2.6
	0.8	0.9	1.4	3.9	2.2	4.5	0.9	(1.5-3)
	3	3	3	3	3	3	3	6
SP13	99.0	78.7	52.8	68.5	52.3	41.4	16.6	2.0
	2.4	2.0	1.7	3.5	2.8	4.2	0.7	(1.5-2.5
	7	7	7	7	7	7	6	14
SP22	103.9	83.5	52.1	70.2	55.4	43.9	17.0	2.5
	1.6	2.8	0.4	2.0	2.7	1.8	0.1	(2-3)
	3	3	2	2	3	3	2	8
SP27	96.8	76.6	51.8	66.2	51.2	39.2	17.8	2.6
	2.8	3.8	1.5	3.9	2.4	3.6	1.0	(2-3)
	8	8	8	8	8	8	6	16

(APP.II.4) FEMALES

AM5	90.4	69.0	50.4	59.9	49.3	35.7	11.2	2.6
	3.2	2.6	1.6	2.5	2.0	2.1	0.4	(1-3)
	10	10	10	10	10	10	10	18
AM6	97.4	75.6	51.7	65.3	54.0	41.1	12.0	2.1
	2.2	1.7	1.2	2.0	1.7	1.1	0.1	(1-3)
	5	5	4	5	5	5	3	10
BA4	90.2	68.3	50.5	58.9	48.4	37.6	10.6	---
	1.9	1.6	1.9	0.6	0.8	1.8	0.4	---
	6	6	6	6	6	6	6	0
ES2	94.4	73.6	49.8	62.2	49.6	38.6	11.0	2.3
	2.7	2.9	1.3	1.0	1.8	0.9	0.3	(2-3)
	5	4	5	5	5	5	4	10
MA1	88.1	67.4	50.2	59.3	47.8	37.7	10.7	2.5
	2.0	2.0	0.9	1.4	1.1	1.3	0.9	(2-3)
	5	5	5	4	5	5	3	12
MG11	92.2	71.0	48.1	62.0	49.7	40.4	10.8	2.0
	1.5	1.2	1.0	1.3	0.4	0.3	0.7	(1-3)
	4	4	4	4	4	4	4	6
MG13	89.3	69.0	50.4	60.0	48.5	36.5	11.3	1.9
	1.3	1.0	1.7	1.0	0.4	1.8	0.5	(1-3)
	6	6	6	4	6	6	5	8
MT9	86.4	66.3	47.6	56.8	48.5	32.7	10.6	2.5
	1.6	1.4	1.0	1.9	2.2	3.0	0.6	(2-3)
	4	4	4	4	4	4	2	8
MT13	91.5	70.1	50.0	58.6	50.4	34.5	10.7	2.2
	4.7	3.4	1.3	2.4	1.3	2.0	0.4	(2-3)
	4	4	4	3	4	4	4	8
PA12	91.5	70.5	51.0	60.8	50.8	36.6	11.3	2.4
	2.0	2.1	1.7	0.8	1.7	1.3	0.6	(1-3)
	12	12	12	11	10	12	10	22
PA13	87.5	67.9	49.2	57.1	47.4	33.7	10.7	2.3
	4.4	2.7	1.2	0.9	2.1	1.7	0.7	(1-3)
	5	5	4	4	5	5	5	12
PA25	89.8	69.0	50.7	58.9	49.4	34.1	10.8	2.2
	2.0	2.0	1.2	1.5	1.6	1.8	0.6	(1-3)
	30	30	31	31	31	31	30	58
PE1	89.2	67.5	48.7	59.2	48.6	38.6	10.7	---
	1.7	1.0	1.2	1.3	2.0	1.6	1.0	---
	6	6	6	6	6	6	6	0
RS1	92.9	70.6	50.8	60.3	48.1	35.2	10.2	1.8
	1.9	2.0	1.4	1.2	1.2	1.7	0.7	(1-2)
	16	17	17	17	17	17	14	28
SC1	96.8	73.5	52.1	62.6	50.2	37.4	11.1	1.8
	1.6	2.6	1.6	2.6	2.4	3.2	0.6	(1-2)
	5	5	5	5	5	5	3	8
SC6	94.6	71.3	51.6	62.1	49.2	36.0	10.3	1.5
	1.4	1.7	1.5	1.2	1.2	0.7	0.7	(1-3)
	8	8	7	7	8	8	8	16
SP3	92.0	71.2	51.4	60.4	48.3	35.2	11.7	2.3
	1.3	1.8	1.2	1.2	3.9	1.6	1.3	(1-3)
	5	5	5	4	5	5	5	10

SP6	93.0	70.5	52.2	62.2	50.2	36.5	11.0	2.5
	1.4	2.4	3.4	2.6	0.9	1.8	0.7	(2-3)
	4	4	4	4	4	4	4	8
SP13	94.3	70.7	51.1	60.8	49.9	37.3	11.4	2.1
	2.4	1.9	1.2	1.0	1.6	1.9	0.7	(1-3)
	11	11	11	11	11	11	10	22
SP22	91.1	69.2	50.2	60.4	48.1	37.1	11.2	2.0
	2.0	2.0	1.9	1.6	1.1	1.7	0.5	(1-3)
	8	7	7	8	8	8	8	22
SP27	91.1	69.7	51.2	60.3	48.1	35.1	11.4	2.4
	2.3	2.7	0.9	1.9	2.0	1.9	0.6	(1.5-3)
	8	8	8	8	8	8	8	16

APPENDIX II.5
SUMMARY OF PELAGE DESCRIPTION FOR CEBUS APELLA.

Pelage is described only for localities from where I examined at least four skins. Cap shape is described only for localities from where I examined at least four adult skins.

Abbreviations:

COLOURS		OTHERS	
R - red	(Ri - reddish)	D.S. - dorsal stripe	
Br - brown	(Bri - brownish)	Vent.- ventral side	
Bl - black	(Bli - blackish)	dist.- distally	
Y - yellow	(Yi - yellowish)		
W - white	(Wi - whitish)	m.e. - more than one specimen	
Gr - grey	(Gri - greyish)	occ. - occasionally	
		gen. - generally	
SEX/AGE			
F - females (*)		spec.- specimen	
M - males (*)			
I - immatures of either sex			

(*) implies adult specimens when printed to indicate sample size

LOCALITY:AM5 (SAMPLE SIZE: 5M,7F)	CAP SHAPE:
PART — COLOUR OF PART	
Tail - Generally Bl distally, occ.dark Br	
Limbs - As tail	
Flanks- Br,Bri,rarely light Br; occ. darker on rump (F); shoulders gen. RiY, occ. RiBr, Y, YiBr or lighter Br	
D.S. - Always noticeable, generally nitid	Either 2 long tufts,
Vent. - Generally R (or R-tinged) chest	two short tufts of no
Cap - Bl, rarely dark Br	tufts.

LOCALITY: AM6 (SAMPLE SIZE: 5M,6F)	CAP SHAPE:
PART — COLOUR OF PART	
Tail - Bl distally, occ. dark Br distally, otherwise as flanks	
Limbs - As tail	
Flanks- Br, RiBr, light Br, dark Br, with RiBr apparently more common. Shoulders gen. RiBr, occ. more Ri than flanks, occ.Br	
D.S. - Always noticeable, generally nitid	
Vent. - R, occ. RiBr (M) or simply lighter	Seems to be always
Cap - Bl gen, BliBr occ.	tuftless.

LOCALITY: BA4 (SAMPLE SIZE: 2M,6F,3I)

PART COLOUR OF PART

Tail - Gen. dark Br distally, occ. Br

Limbs - Gen. dark Br distally, occ.Br; as flanks basally

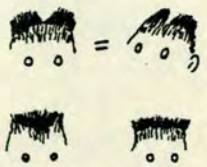
Flanks- Gen.light Br, occ. GriBr tinged with Ri; shoulders lighter or YiBr

D.S. - When noticeable, only slightly so; occ. more Ri

Vent. - YiBr, Ri light Br, RiYiBr or RiBr

Cap - Br, dark Br or BliBr

CAP SHAPE



Bent backwards, not always divided, light colours at hair base

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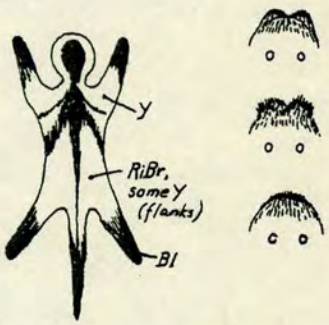
LOCALITY: BA5 (SAMPLE SIZE: 2M,1F,3I)

CAP SHAPE & PELAGE COLOUR PATTERN:



PART COLOUR OF PART

Tail - Dark Br or BliBr distally; basally with many Yi hairs, or with RiBr patches

Limbs - Gen. BliBr distally, occ. posterior limbs darker; occ. light-coloured hairs interspersed

Flanks- Darker, shinier coat anteriorly (BliBr) lighter colour posteriorly (RiBr); Yi shoulder; (see drawing)

D.S. - not evident

Vent. - few notes taken; R in one specimen

Cap - YiBr anteriorly, darker Br posteriorly; occ. these two shades form patches; lighter-coloured hairs anteriorly

Hairs of cap are bent backwards and may or not form two tufts; tufts are gen. not very distinct.

LOCALITY: ES2 (SAMPLE SIZE: 6F,3M,10I)

CAP SHAPE:

PART COLOUR OF PART

Tail - BliBr distally; basally as flanks

Limbs - As tail

Flanks- RiBr or Br with some R; occ.GriBr anter. RiBr posterirly;shoulders may be lighter in colour

D.S. - generally not noticeable; occ. a wide rufous stripe may be seen

Vent. - gen. RiBr; occ.R or Br tinged with R

Cap - gen. BliBr, occ. very dar Br

Two tufts converge to form a median one. See also fig. II.5.

LOCALITY: MA1 (SAMPLE SIZE: 2F,7M,1I + 2 indiv. of indet. sex)

PART	COLOUR OF PART
Tail	Br distally, light Br otherwise, darker dorsally
Limbs	distally: gen. light Br, occ. Br
Flanks	YiBr or Yi light Br; occ. RiBr, light Br or YiBr tinged with R; shoulder may be lighter in colour
D.S.	either not present or not nitid
Vent.	few notes taken; may be Ri light Br
Cap	gen. dark Br; occ. Br

CAP SHAPE:

Tufts not very distinct; hairs bent backwards.

LOCALITY:MG4,left margin SAMPLE SIZE: 2M,1F

PART	COLOUR OF PART
Tail	BliBr; tip always Bli
Limbs	m.e. Br; may be RiBr with Bli extremity
Flanks	gen. RiBr, occ. light Br
D.S.	not perceptible
Vent.	very variable; BliBr, GriY, strong R
Cap	BliBr or Bl

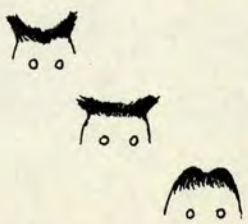
CAP SHAPE:

Two tufts converge to form a median one

LOCALITY: MG9 (SAMPLE SIZE: 4M,2F,2I)

PART	COLOUR OF PART
Tail	patchy Br to Bli, or occ.Br with Bli dorsally
Limbs	as tail, varies from Br to Bli; patchy appearance. In F dark Br or Br
Flanks	may include dark Br, Br and Bli in patches, or be only light Br or only Br
D.S.	Gen. dorsal area slightly darker than flanks
Vent.	m.e. YiBr (notes not taken for all spec)
Cap	dark Br to Bli, occ. tinged with Ri

CAP SHAPE:



Tufts may be very distinct or hairs may be bent backwards

LOCALITY: MG11=21 (SAMPLE SIZE: 5M,4F)

PART	COLOUR OF PART
Tail	dark Br or BliBr
Limbs	as tail; gen. dark Br to Bli distally
Flanks	Quite variable; GriBr, light Br to Br, or Br with patchy appearance; shoulders and throat may be lighter in colour
D.S.	not very evident; occ.indistinguishable
Vent.	lighter colour (as compared to flanks)
Cap	dark Br or BliBr

CAP SHAPE:

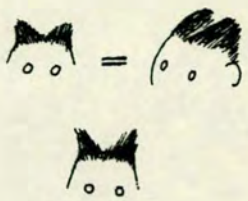
Quite variable; tuft may be bent backwards, or be an intermediate between ES-2 type and other types.

LOCALITY: MG13+14 (SAMPLE SIZE: 6F,8M)
(includes the type of versuta)

PART — COLOUR OF PART

Tail - Br to BliBr,occ.darker dorsally,Ri vent.
Limbs - Post.limbs as tail; ant.limbs Br or,less often, dark Br distally
Flanks- gen.light Br,may be Gri light Br, occ. tinged with Ri posteriorly; shoulders occ. lighter in colour
D.S. - dorsal part may be slightly darker than flanks; D.S. gen. not distinguishable.
Vent. - Yi, light Br, or orange- or R- tinged
Cap - gen.dark Br or Bli Br, occ. Br

CAP SHAPE:



Two well formed tufts bent backwards(M) or erect(F)(M)

LOCALITY: MT3 (SAMPLE SIZE: 2M,1F, +1 spec.with unknown age)

PART — COLOUR OF PART

Tail - As limbs; D.S. visible
Limbs - Variable; GriBr, or Ri, or Yi
Flanks- YiBr or heterogeneous GriBr or GriYiBr
D.S. - broad & evident; visible; hardly visible
Vent. - some R; lighter ventrally
Cap - BliBr

CAP SHAPE:

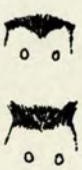
Tufts are not long

LOCALITY: MT-8 (SAMPLE SIZE: 3M,2F,2I +1 spec.with unknown age)

PART — COLOUR OF PART

Tail - Br or light Br, darker distally
Limbs - Br
Flanks- light Br or heterogeneous YiBr
D.S. - if discernible, not well defined
Vent. - RiY or Yi
Cap - dark Br

CAP SHAPE:



Tufts may be long or not

LOCALITY: MT-9 (SAMPLE SIZE: 1M,4F,2I)

PART — COLOUR OF PART

Tail - light Br or Br; may be darker dorsally
Limbs - GriBr, darker distally
Flanks- m.e. GriBr; may be Gri light Br
D.S. - if discernible, not well defined
Vent. - tinged with Yi or RiY
Cap - from Br to BliBr

CAP SHAPE:

Tufts may be long or not

LOCALITY: MT-13 (SAMPLE SIZE: 5M,4F+1M of unknown age)

PART COLOUR OF PART

Tail - Br to dark Br,darker dorsally. Colour is not uniform (darker in some portions)

Limbs - Br mixed with dark Br; some parts of the coat are lighter or darker in colour - pelage is not uniformly coloured.

Flanks- Gen. Gri light Br,may be slightly tinged with orange or yellow (particularly towards ventral side);or more Gri towards dorsal side.

D.S. - poorly defined but can be distinguished

Vent. - light Br tinged with orange;Yi light Br

Cap - dark Br to Bl

CAP SHAPE:

Gen. tufts are not long & are bent backwards, but one old indiv. had long erect tufts.

LOCALITY: PA-1 (SAMPLE SIZE: 2M,4F,1I)

PART COLOUR OF PART

Tail - Bl distally

Limbs - Gen. Bl distally; occ. Br

Flanks- Bri, with Y shoulders

D.S. - Present

Vent. - (data not collected)

Cap - Black

CAP SHAPE:

2 tufts may be formed, long or not, or tufts may be absent

LOCALITY: PA2=5 (SAMPLE SIZE: 3M,3F +1M of unknown age)

PART COLOUR OF PART

Tail - Bl distally, occ. with some R hairs

Limbs - Bl distally

Flanks- light Br,may be more Ri posteriorly; shoulders Y or Yi light Br with some Ri

D.S. - Present, not necessarily very nitid

Vent. - (data not collected)

Cap - Bl

CAP SHAPE:

Two tufts generally formed, not necessarily long

LOCALITY: PA8+17 (SAMPLE SIZE: 7M,1F +4M of unknown age)

PART — COLOUR OF PART

Tail - Bl distally, with some R hairs
Limbs - As tail
Flanks- Gen.RiBr, occ.Bri; shoulders lighter in colour than flanks, gen. Y
D.S. - Present, not necessarily very nitid
Vent. - (data not collected)
Cap - Gen. Bl, but may be Br

CAP SHAPE:

—

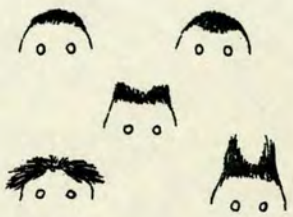
Tufts may be formed or not; if formed, gen. not long.

LOCALITY: PA-12 (SAMPLE SIZE: 13F,12M,5I & 2M of unknown age)

PART — COLOUR OF PART

Tail - BliBr gen.; DS may be present at base
Limbs - BliBr gen.; sometimes (M) R hairs mixed
Flanks- Light Br gen., with shades of Yi, Ri or Gri. Shoulders Yi light Br, Ri light Br or YiRi.
D.S. - Present; occ. wide and not very nitid; may be RiBr rather than darker Br
Vent. - R or RiBr; may be YiBr or RiYiBr
Cap - from dark Br to BliBr

CAP SHAPE:



Long tufts are only occ.(15% of spec.);occ. very erect (F)

LOCALITY: PA-13 (SAMPLE SIZE: 4F,5M,6I)

PART — COLOUR OF PART

Tail - Dark Br to Bli distally, some Ri basally
Limbs - As tail
Flanks- GriBr or light Br, sometimes YiBr; shoulders gen. YiBr, occ. RiBr or Y
D.S. - Present, occ.more Ri posteriorly (M)
Vent. - RiBr
Cap - More often dark Br;may be BliBr

CAP SHAPE:

Tufts gen.not present,but one animal had long/erect tufts.

LOCALITY: PA-24 (SAMPLE SIZE: 3F,2M)

PART — COLOUR OF PART

Tail - Bl
Limbs - Bl
Flanks- Br, YiBr or Br with Bl hair-tips (although each ind.is one shade of Br, the tendency is for a not too dark Br)
D.S. - gen. not well defined
Vent. - May be strong orange
Cap - Bl

CAP SHAPE:

Tufts occ.long, not necessarily well separated into two tufts

LOCALITY: PE-1 (SAMPLE SIZE: 2M,6F)

PART	COLOUR OF PART
Tail	- light Br, only slightly darker distally, sometimes darker patches; mixed with light-coloured hairs
Limbs	- as tail
Flanks	- Gri or Yi light Br
D.S.	- Not well defined; at most weakly defined
Vent.	- Gen. Yi light Br, occ. YiRi light Br
Cap	- not dark Br

CAP SHAPE:

Tufts not long, and bent backwards. Light-coloured hairs at anterior end.

LOCALITY: PR-5 (SAMPLE SIZE: 1M,3F,1I)

PART	COLOUR OF PART
Tail	- dark Br to BliBr
Limbs	- gen.BliBr, parts occ. GriBr or light Br
Flanks	- Gen. GriBr;may be dark Br or Gri dark Br F may have white hairs mixed in the coat particularly at anterior parts
D.S.	- no clear D.S., but back may be slightly darker than flanks
Vent.	- gen. Yi; colour lighter than flanks
Cap	- gen. BliBr

CAP SHAPE:

Long tufts are common

LOCALITY: PR-6 (SAMPLE SIZE: 1M,3F,2I)

PART	COLOUR OF PART
Tail	- gen. dark Br or dark to BliBr; occ.GriBr (occ.with patchy appearance)
Limbs	- as tail
Flanks	- gen.dark Br to GriBr; may be Br, GriBr to Br (occ. with patchy appearance) There may be W hairs mixed with coat, particularly anterior part (F)
D.S.	- no clear D.S.; occ. post.part of back is darker than flanks.
Vent.	- lighter than flanks; YiW, YiBr
Cap	- gen. BliBr, occ.dark Br

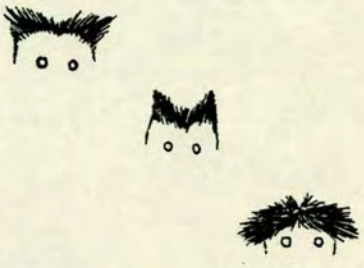
CAP SHAPE:

Long tufts are common

LOCALITY: SC1 to 3 (SAMPLE SIZE: 2M,3F +1 of unknown sex; includes the type of C.caliginosus)

PART	COLOUR OF PART
Tail	- gen. BliBr, but may be dark Br
Limbs	- as tail
Flanks	- dark Br or BliBr; F may have white hairs mixed with the coat
D.S.	- no clear D.S.
Vent.	- dark tip hairs;general aspect Br to BliBr
Cap	- BliBr

CAP SHAPE:



Long tufts are common; tufts may be torsioned sideways

LOCALITY: SC4 (SAMPLE SIZE: 2M,2F)

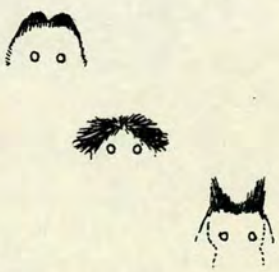
PART	COLOUR OF PART
Tail	- BliBr, occ. light tip of hairs
Limbs	- From dark Br to BliBr,occ.light tip hairs
Flanks	- BliBr
D.S.	- no clear D.S.;post.part may be darker
Vent.	- colour lighter than flanks; may be Yi,Ri
Cap	- BliBr

CAP SHAPE:

LOCALITY: SP12(+32) (SAMPLE SIZE: 3M,2F) (plus more than 30 animals observed in the wild)

PART	COLOUR OF PART
Tail	- darkBr to BliBr, distal part darker;D.S. may be occ. seen
Limbs	- darkBr to BliBr, distal part darker; may have patchy aspect
Flanks	- various shades of Br or of GriBr; may have patchy aspect
D.S.	- occ.visible posterior part back
Vent.	- quite variable; may be RiY,Ri light Br, often with tip of hairs of dark colour
Cap	- gen. BliBr; ears often noticed to have light coloured hairs

CAP SHAPE:



Long tufts common; they may be torsioned sideways

LOCALITY: SP13+18 (SAMPLE SIZE: 3M,6F,4I)

PART — COLOUR OF PART

Tail - BliBr or dark Br; occ.mixed with YiR hairs; D.S. may be obs. occ.
Limbs - as tail; may have a patchy aspect
Flanks- various shades of Br, from light to dark and also may be GriBr, RiBr, or have a patchy aspect
D.S. - gen.no clear D.S.; occ. weakly defined
Vent. - quite variable; may be RiBr,YiBr(chest), YiBr with Bli tips, or simply Br
Cap - from dark Br to Bli, gen. Bli Br

CAP SHAPE:

Long tufts common

LOCALITY: SP-20 (SAMPLE SIZE: 2M,2F,1I)

PART — COLOUR OF PART

Tail - BliBr, dark Br, heterogeneous Br
Limbs - as tail
Flanks- Br, YiBr, GriBr, GriBr to Br
D.S. - gen. no clear D.S.; occ. a wide strip
Vent. - YiBr, or simply lighter than flanks
Cap - BliBr

CAP SHAPE:

Long tufts common

LOCALITY: SP-22 (SAMPLE SIZE: 2M,4F,nI)

PART — COLOUR OF PART

Tail - Br,dark Br,BliBr;may have patchy aspect
Limbs - as tail
Flanks- Br with some darkBr, or only Br
D.S. - D.S., if present, not well defined
Vent. - Yi lightBr, Ri lightBr, or lighter than flanks
Cap - dark Br or BliBr

CAP SHAPE:

Long tufts common

LOCALITY: SP-27 (SAMPLE SIZE: 9M,7F,1I)

PART — COLOUR OF PART

Tail - gen. dark Br; may be BliBr
Limbs - gen. dark Br, occ. dark to BliBr dist.
Flanks- GriBr, or Br, or Br to GriBr; hips may be tinged with RiBr
F may have W hairs ant. part of flank
D.S. - If present, not very well defined
Vent. - YiBr,orange,RiBr,YiWi,light Y or light Br
Cap - from dark Br to BliBr

CAP SHAPE:

(see Fig.II.5, top row)

Long tufts common

LOCALITY: SP-28 (SAMPLE SIZE: 2M,2F,1I)

PART	COLOUR OF PART
Tail	- dark Br or BliBr, occ. lighter Br
Limbs	- Gri to BliBr, or light Br to Br
Flanks	- gen. GriBr, or Gri dark Br F may have W hairs mixed with darker hairs of back
D.S.	- if present, not very well defined
Vent.	- YiR or Yi
Cap	- BliBr or dark BliBr

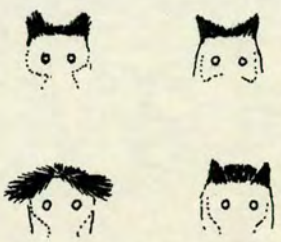
CAP SHAPE:

Long tufts common

LOCALITY: SP-33 (SAMPLE SIZE: around 20 animals observed in the wild)

PART	COLOUR OF PART
Tail	- BliBr
Limbs	- BliBr
Flanks	- Gri dark Br or GriBr
D.S.	- not evident
Vent.	- tinged with orange in several individuals
Cap	- BliBr

CAP SHAPE:

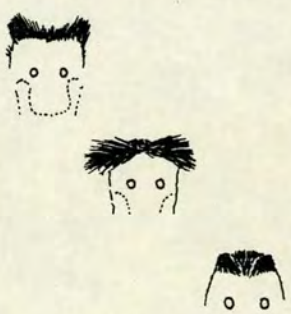


Long tufts common; tufts may be torsioned sideways

LOCALITY: SP-36 (SAMPLE SIZE: around 20 animals observed in the wild)

PART	COLOUR OF PART
Tail	- BliBr
Limbs	- BliBr
Flanks	- Varies from homogeneous dark Br to Gri light Br
D.S.	- not evident
Vent.	- either Yi light Br, tinged with orange, or tinged with R
Cap	- BliBr; ears noticed to have many light coloured hairs

CAP SHAPE:



Long tufts common; tufts may be torsioned sideways

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LISPB – V. Studies of crustal shear waves

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Summary. Many shots in the LISPB profiles produced shear waves with large amplitudes which were recorded by three-component stations. However, S waves seem to be strongly attenuated when they propagate through complex velocity structures. Upper crustal refractions (mainly land shots) and wide-angle reflections (mainly sea shots) were picked with the help of particle motion plots. S to P travel-time ratios (t_s/t_p) were used to calculate the distribution of Poisson's ratios in a crustal model. The results were generally close to $\sigma = 0.25$ except in the upper crust south of the Southern Uplands Fault ($\sigma = 0.231$) and in the middle crust under the Midland Valley ($\sigma = 0.224$).

1 Introduction

A knowledge of the distribution of Poisson's ratio (or alternatively V_p/V_s) might be expected to add significantly to our understanding of the physical properties of, and processes in, the crust and upper mantle. However there is little published work on this subject presumably due to the difficulties of recording shear waves and picking their onsets accurately.

This paper describes the study of the S waves generated in some of the LISPB profiles (Bamford *et al.* 1976; Bamford *et al.* 1978), in particular on the segments ALPHA and BETA in Scotland (Fig. 1), and complements the determination of P wave velocity structure on segments ALPHA, BETA and GAMMA (Bamford *et al.* 1978). Conventionally Poisson's ratio (σ) is determined by the ratio of the apparent velocities of P and S waves at the surface with results usually in the range 0.23 to 0.27 but with large uncertainties of 0.01 or greater. The LISPB observations on closely spaced three-component stations allows σ to be determined with better accuracy than 0.01.

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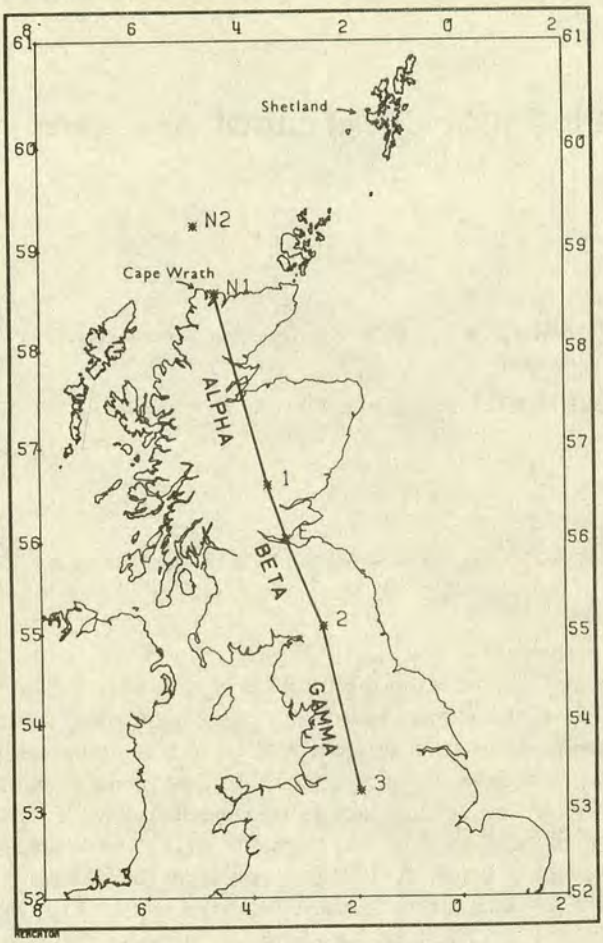

Figure 1. Location of shots and profiles.

2 Data quality

Not all of the LISPB shots generated good *S* waves but most shots recorded on ALPHA and BETA produced some shear waves either as upper crustal refractions (shots 1, E and 2; e.g. Fig. 2(a)) or as wide-angle reflections (shots N2, N1, 1 and E recorded on ALPHA, e.g. Fig. 2(b)).

The quality of *S* waves on segment GAMMA is far inferior to that on ALPHA and BETA and it seems that a relatively complex structure beneath GAMMA (Bamford *et al.* 1978) may be responsible. *S* waves may be easily attenuated by propagating through a structure with many velocity discontinuities. This could explain why land shot 2 (Fig. 2(a)) produced the best signal to noise ratio for *S* waves when recorded to the north (BETA) but no *S* waves when recorded to the south (GAMMA). Similarly, shot E produces reasonably clear *S* waves to the north (in the Midlands Valley and on ALPHA) to distances of 90 km whereas to the south the *S* waves are very poor, perhaps because of complex structure at and south of, the Southern Uplands Fault. In contrast, the absence of Moho reflections on both BETA and GAMMA may be due to the anomalous Moho transition identified by Bamford *et al.* (1978). No shear refractions from the Moho (conventionally called S_n) were detected on any of the crustal profiles.

The same notation has been adopted for *S* crustal phases as was used for *P* crustal phases by Bamford *et al.* (1978). Thus a_0 and a_1 are upper crustal refractions, e is a wide-angle reflection from the lower crust and c is the wide-angle Moho reflection.

3 *S* travel-time data

Record sections of those parts of the seismograms that might contain *S* were constructed with reduction velocity 3.464 km/s ($=6.0/\sqrt{3}$). For each shot there were three sections: one for the vertical, one for the radial horizontal and one for the transverse horizontal components (e.g. Fig. 2). A preliminary identification of *S* waves was made based on travel times using the *P* seismic sections as reference and assuming an average Poisson's ratio close to 0.25.

A time window of a few seconds and including the suspected *S* arrivals was then selected for each station for the plotting of particle motion diagrams: these diagrams show the ground motion in the sagittal plane (vertical-radial) and in the horizontal plane (radial-transverse). For this purpose the original records were filtered with a lowpass Hanning window, instead of a bandpass. This reduces the high-frequency background noise and at the same time does not diffuse the *S* onsets with the 'ringing' often caused by narrowband filters. The three components and the particle motions were then plotted and used for picking *S* arrivals, the vertical and radial components giving an *SV* onset and the transverse component an independent *SH* onset.

Not all stations had *S* waves with amplitudes large enough to be read. Out of 102 stations recording *P* arrivals for crustal refractions on profiles 1 – ALPHA, 1 – BETA, E – BETA + ALPHA, 2 – BETA, about 70 per cent produced *S* arrivals with a signal to noise ratio (SNR) large enough so that either *SV* or *SH* could be picked. Fig. 3 shows examples of *S* wave onsets of phase a_0 from profile 2 – BETA (for simplicity diagrams of particle motion in the horizontal plane were omitted).

It is known theoretically that the ground motion of *S* waves in a homogeneous half-space is not always linear but can be elliptical for shallow angles of emergence at the surface (e.g. Nuttli 1961; Meissner 1965). For example *SV* ground motion is elliptical for emergence angles (measured from the horizontal) less than 54.7 or 57.7° for Poisson's ratio 0.25 or 0.30 respectively. Non-linear *SV* ground motion was sometimes observed in the LISPB stations as illustrated in Fig. 3. More often the ground motion of the *S* wave train is more complicated than the examples in Fig. 3. The character of the *SV* and *SH* ground motion sometimes changes completely between adjacent stations, indicating that it is strongly affected by the structure very close to the surface (1 or 2 km beneath the station). For this reason no special processing could be applied to pick or enhance the *S* waves, like polarization filters (e.g. Montalbetti & Kanasewich 1970), where the same kind of ground motion would have to be assumed for all stations. Instead *SV* was picked with the help of particle motion plots as any motion with a phase difference between vertical and radial components ranging from 180° (linear motion) to ±90° (elliptical motion). The uncertainties in the *S* onsets varied approximately from $\pm T/4$ (good SNR) to $\pm T$ (poor SNR), where *T* is the main period of the *S* waves. Thus, land-shot arrivals for upper crustal phases (Fig. 2(a)) can have onsets accurate to about ±0.1 s or better whereas deeper penetrating arrivals for sea shots (Fig. 2(b)) can be determined to within ± 0.2 to ± 0.3 s.

4 Travel-time ratios (t_s/t_p)

For each station and for each phase, *S* travel times t_s were divided by the corresponding *P* travel time t_p and these ratios t_s/t_p were plotted against distance from the shot.

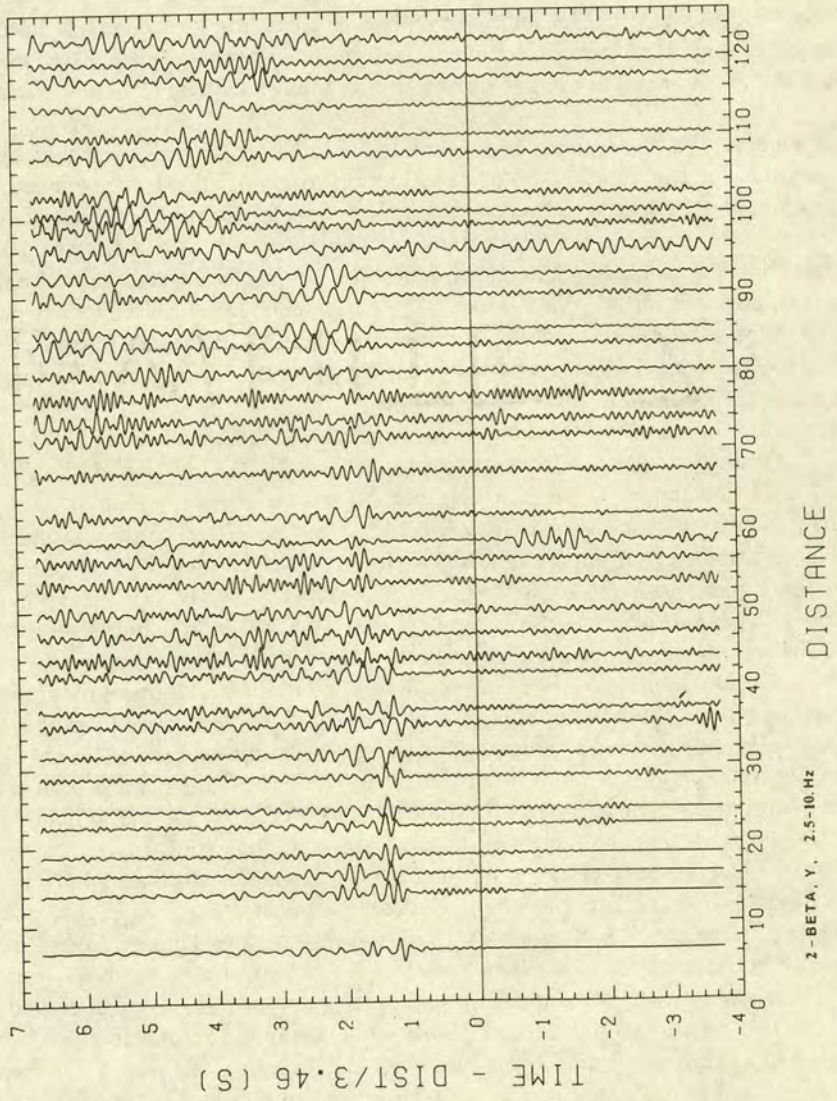

Figure 2 (a)

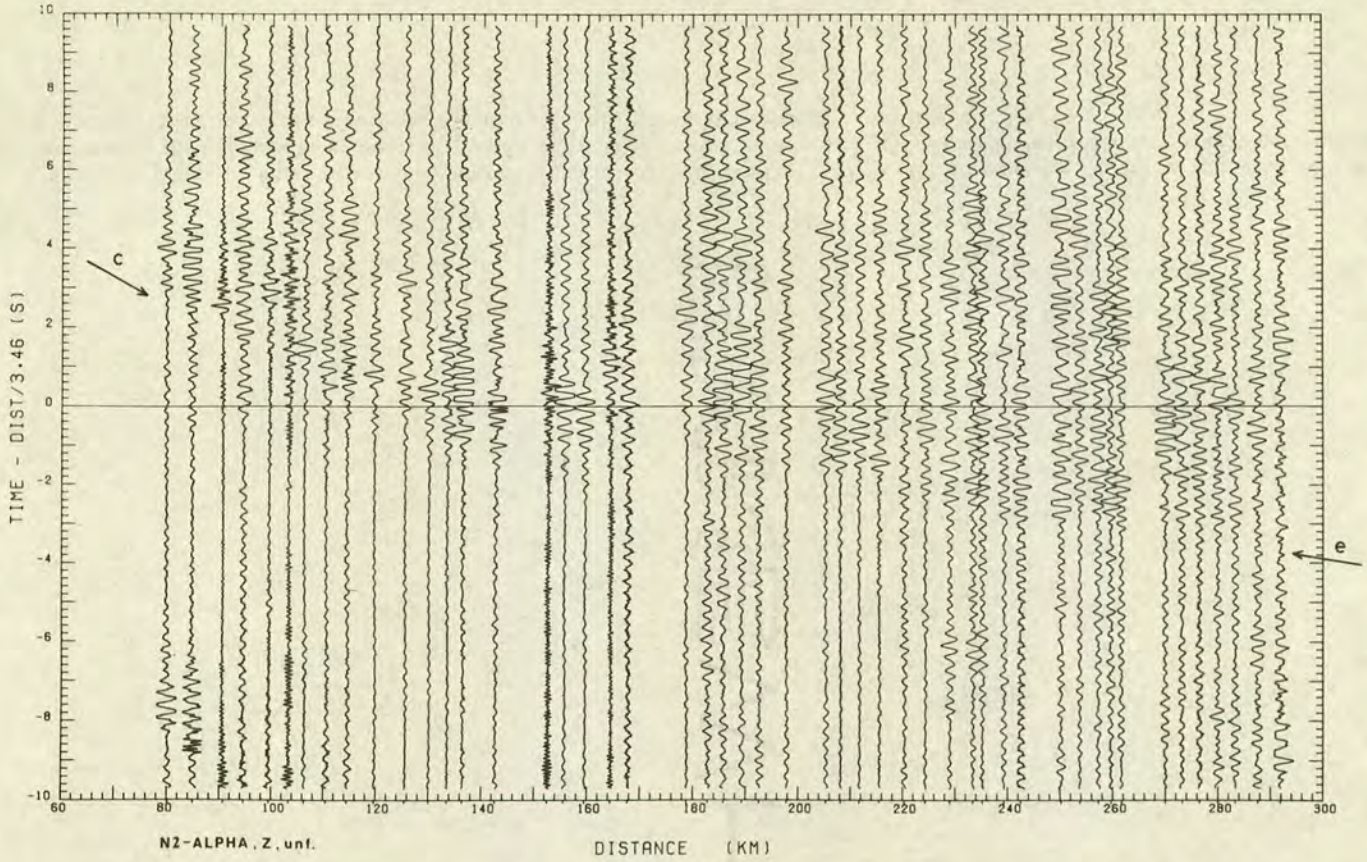

Figure 2 (b)

Figure 2. (a) Seismic section of shear waves, profile 2 – BETA (shot 2 recorded on segment BETA). Transverse component, bandpass filtered 2.5–10 Hz. The phase at about 1 s reduced time up to 100 km distance is a_0. (b) Seismic section of shear waves, profile N2 – ALPHA. Vertical component, unfiltered. Arrows indicate direction of phases c and e.

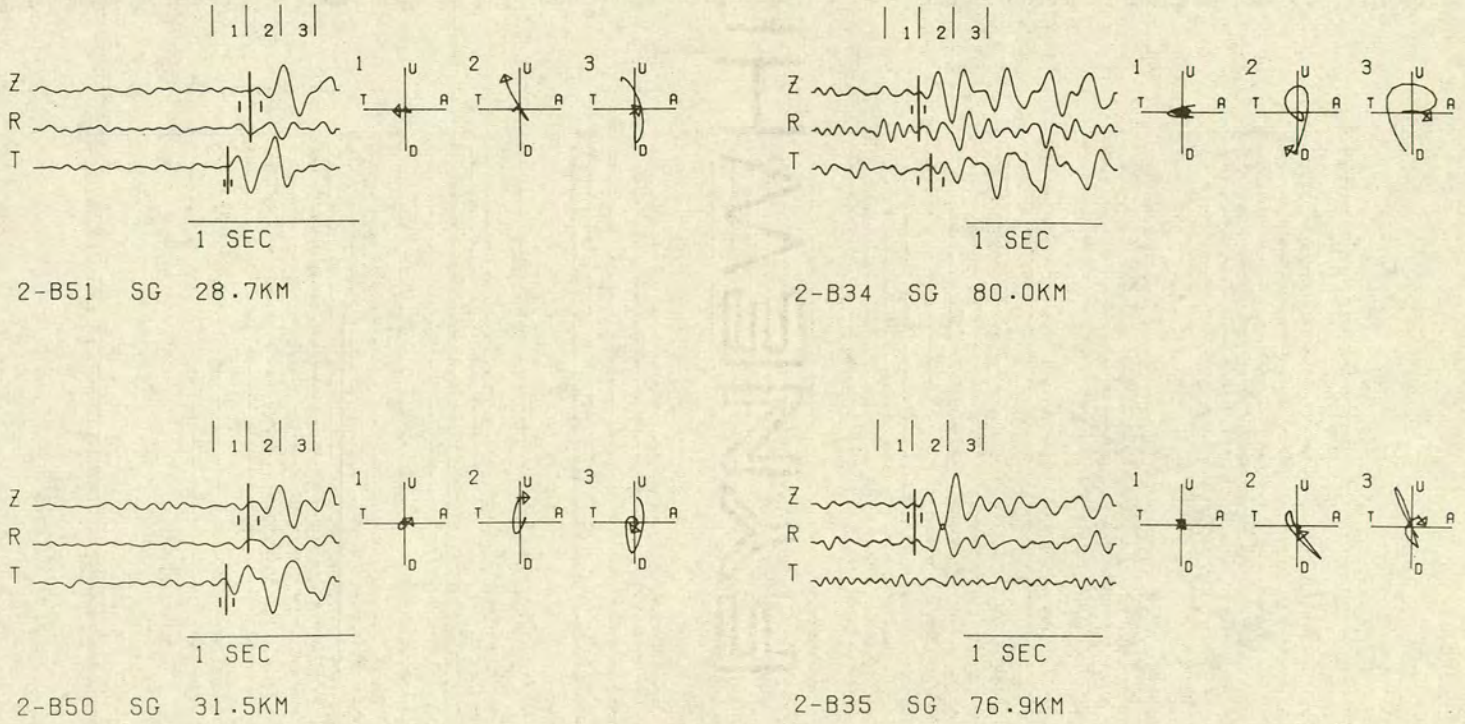

Figure 3. Examples of *S* arrivals and particle motion plots (*Z*–*R* plane). Phase a_0, profile 2 – BETA. The lines crossing the vertical and radial (*R*) components are *SV* picks, those crossing the transverse components (*T*) are *SH* picks. The two small lines on each side of the pick indicate its uncertainty. Particle motion diagrams refer to time windows marked on top of seismograms. U = up; D = down; T = towards the shot; A = away from the shot.

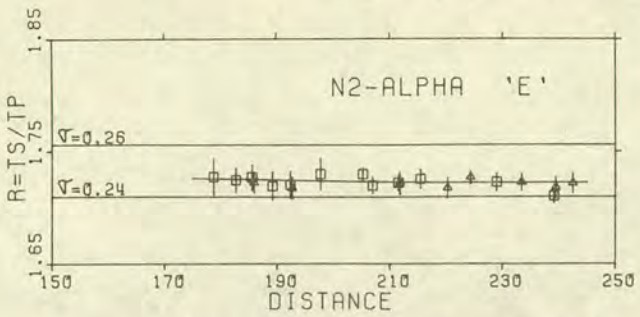

Figure 4. t_s/t_p travel-time ratio of phase e, profile N2 – ALPHA. The two horizontal lines were drawn at those values of t_s/t_p corresponding to $\sigma = 0.26$ and 0.24. The curve through the data is the theoretical curve from the model shown in Fig. 7. *SV* and *SH* data are indicated by squares and triangles respectively.

Fig. 4 shows a t_s/t_p plot for phase e from shot N2 (reflected from the bottom of layer 2, Fig. 7). The curve through the data points is the theoretical t_s/t_p curve given by the model to be explained below. Fig. 5 shows t_s/t_p plots for the upper crustal refractions (phase a_0 and a_1).

In the case of the crustal refractions, all shots have the same general trend of high t_s/t_p near the shot, decreasing with distance. This is explained by high values of σ near the surface, especially in sedimentary basins like the Midland Valley (Fig. 7, between HBF and SUF) and the Northumberland basin (Shot Point 2). Near the shot t_s/t_p is largely affected by the high σ of sediments, but as the waves travel longer distances in the refractor, below the sediments, the final t_s/t_p approaches the *P* to *S* velocity ratio of the refractor, which is lower than that of the sediments.

High values of σ in sediments, or generally near the surface, is the rule rather than the exception, as indicated by many field measurements like those of Jolly (1956); Erickson, Miller & Waters (1968); Geyer & Martner (1969); Tatham & Stoffa (1976) and Scarascia, Colombi & Cassinis (1976).

Laboratory measurements of Poisson's ratio in dry sandstones and limestones have a very wide range (e.g. King 1966; Gregory 1976) and are usually less than 0.25. However, rocks are usually porous and when specimens are filled with fluid, which is probably closer to the average condition in the field, then σ can increase significantly (King 1966; Gregory 1976). A small proportion of soft and unconsolidated sediments near the surface will also contribute to high average values of σ (Scarascia *et al.* 1976; Gregory 1976). So, Poisson's ratios as high as 0.33 near the surface as required by t_s/t_p data (see results below) are in general agreement with laboratory and field measurements.

5 Inversion of t_s/t_p ratios

It was not possible to use only the *S* wave data to get an independent model of *S* velocity structure, especially depths of boundaries, primarily because of the incompleteness of *S* refraction data and uncertainties in the *S* onsets. The following procedure was then used to calculate values of Poisson's ratios in a crustal model to fit all available t_s/t_p data.

The *P* velocity model suggested by Bamford *et al.* (1978) for Northern Britain was used as a reference. That model allows a small range of possible velocities in each layer. For the present purposes, we have used values from within the range which tend to be suggested by some additional modelling (especially ray-tracing) we have carried out. This reference model is shown in Fig. 6. One modification was made however under shot point 1 where the super-

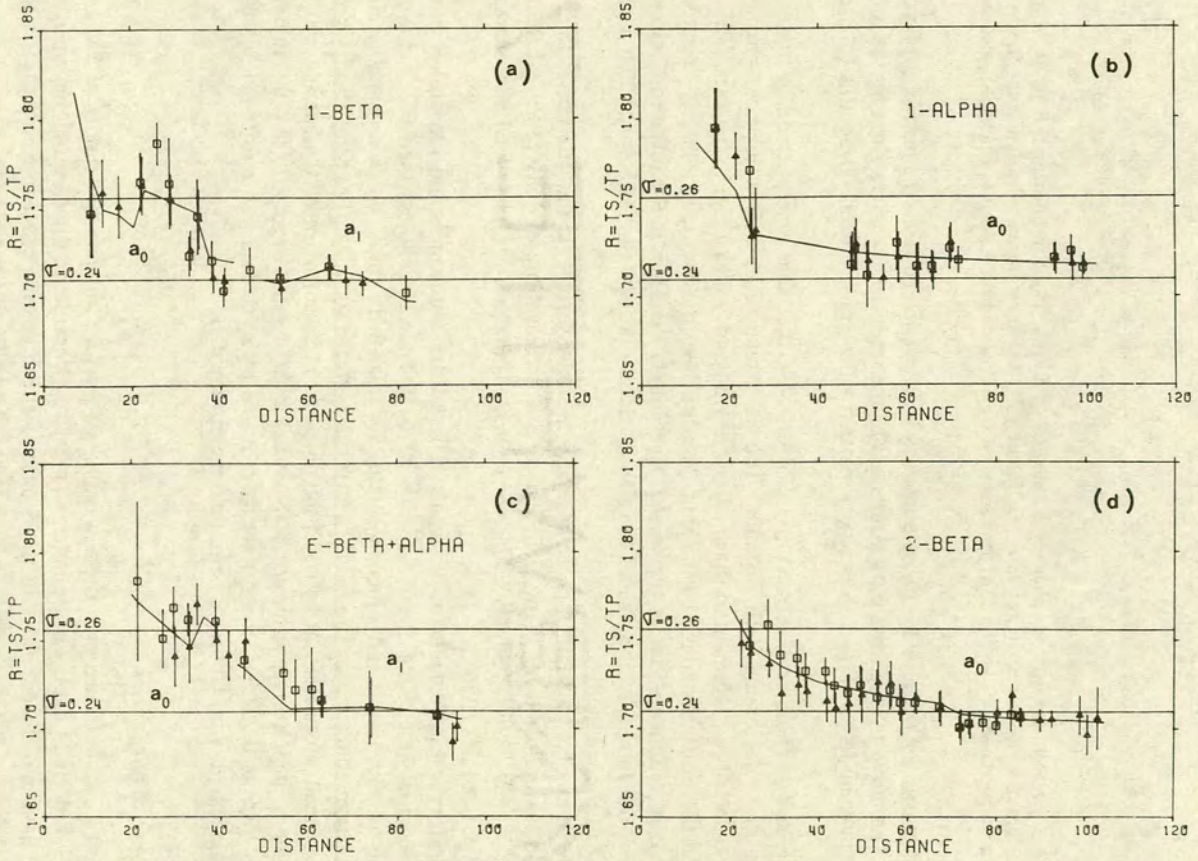

Figure 5. t_s/t_p travel-time ratios for crustal refractions. a_0 and a_1 refer to refractions through layers 1 and 2 respectively. Symbols as in Fig. 4.

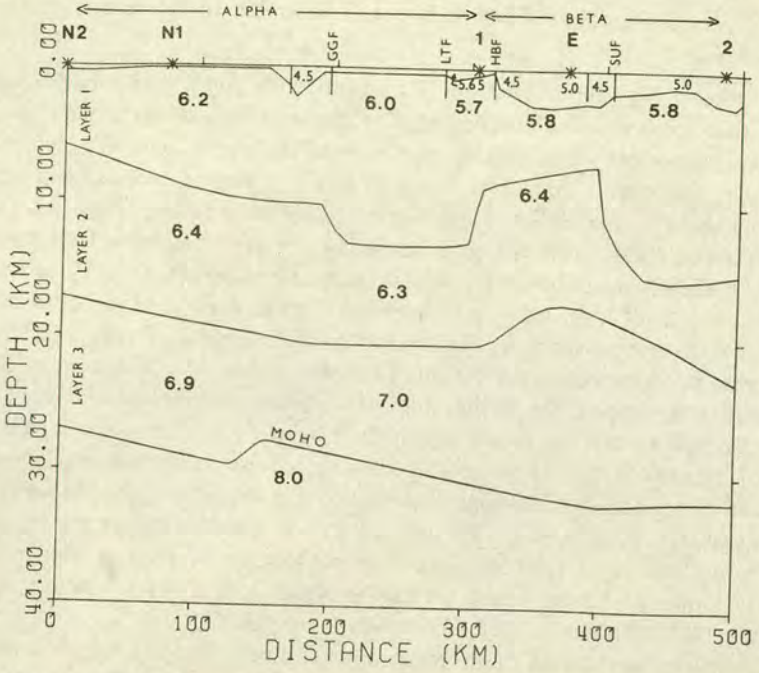

Figure 6. Reference crustal model for segments ALPHA and BETA (after Bamford *et al.* 1978) with *P* velocities in km/s. GGF, LTF, HBF, SUF, are Great Glen, Loch Tay, Highland Boundary and Southern Uplands Faults, respectively. Vertical exaggeration 10:1.

ficial layer of velocity 5.0 km/s and 0.2 km thickness was arbitrarily substituted by one dipping north with *P* velocity 5.65 km/s and thickness of 0.5 km (beneath shot 1). This is not in contradiction to the model of Bamford *et al.* because the scale of the LISPB experiment does not allow resolution of such details. Both models are equivalent in that they give about the same *P* travel times for stations near shot 1. Such a modification was found necessary in order to account for the t_s/t_p of stations within 15 km either side of shot 1.

The crustal layers were divided vertically into blocks with constant *P* velocities. The inversion of all t_s/t_p data to obtain Poisson's ratio σ in each block was done in two stages: (a) an initial model was found by a detailed trial and error search, and (b) the initial model was improved iteratively by a least-squares procedure. In the second stage the t_s/t_p functions were linearized with respect to their parameters σ by a Taylor-series expansion, and all profiles and phases (refractions + reflections) were used simultaneously in the inversion. Data from shots 1 and E, for example, had a reduced chi-square $\chi^2_\nu = 1.23$ (84 degrees of freedom) in the initial model; the solution of the first iteration had $\chi^2_\nu = 0.77$ and the process converged in the second iteration which gave results identical to the first.

Theoretical travel times for the t_s/t_p curves were calculated using an average horizontal-plane layer model allowing different layerings under the shot and under each station. Depths and *P* velocities were taken from the reference *P* velocity model.

The advantage of this method for calculating Poisson's ratios is that it is not critically dependent on an accurate *P* velocity model. Thus *P* velocities could be wrong by ± 0.1 km/s without affecting the theoretical t_s/t_p values at all. In this way, Poisson's ratios can be determined, particularly in the upper crust, with greater accuracy than by calculating *P* and *S* velocity independently and then forming the ratio of the two.

However, two assumptions have been made in order to determine Poisson's ratio structure. These are:

(i) That σ, as a first approximation, is constant with depth within each crustal block. This means that the σ value determined by a refraction which travels in the uppermost part of the refractor layer can be used as representative of the whole layer. For layer 1 under the Midland Valley (between shot points 1 and E) this is a reasonable assumption considering that σ is only slightly affected by changes in confining pressure and temperature for depths greater than about 4 km. For a change in confining pressure from about 1 kb (depth around 4 km) to 2 kb (depth around 8 km), σ usually increases by less than 0.005 (Simmons 1964; Christensen 1965, 1966). An increase in σ of 0.005 from the top to the bottom of layer 1 would produce an increase in t_s/t_p for refractions from layer 2 of only 0.001 in terms of Poisson's ratio, at distances around 50 km. Temperature has little effect on σ (Birch 1969) and a difference in temperature of the order of 40°C between depths of 4 and 8 km would produce a decrease in σ of less than 0.001, if Birch's results for olivine could be used only as an order of magnitude for upper crustal material. These values are much less than the measurement errors due to travel-time inaccuracies. On the other hand, between the Great Glen Fault and shot point 1 (Fig. 7) σ may not be constant throughout the whole depth of layer 1. From 2 km depth (probable depth of penetration of phase a_0) where pressure is about 0.5 kb down to 12 km where pressure is about 3 kb, Poisson's ratio could increase by as much as 0.010 (Simmons 1964; Christensen 1965, 1966).

(ii) That an average Poisson's ratio over a crustal block tens of kilometres long (or even more than a hundred kilometres long) is a good representation, as a first approximation, of the actual distribution of σ along the block. This hypothesis can only be tested by checking how well the theoretical t_s/t_p curves fit the observed data.

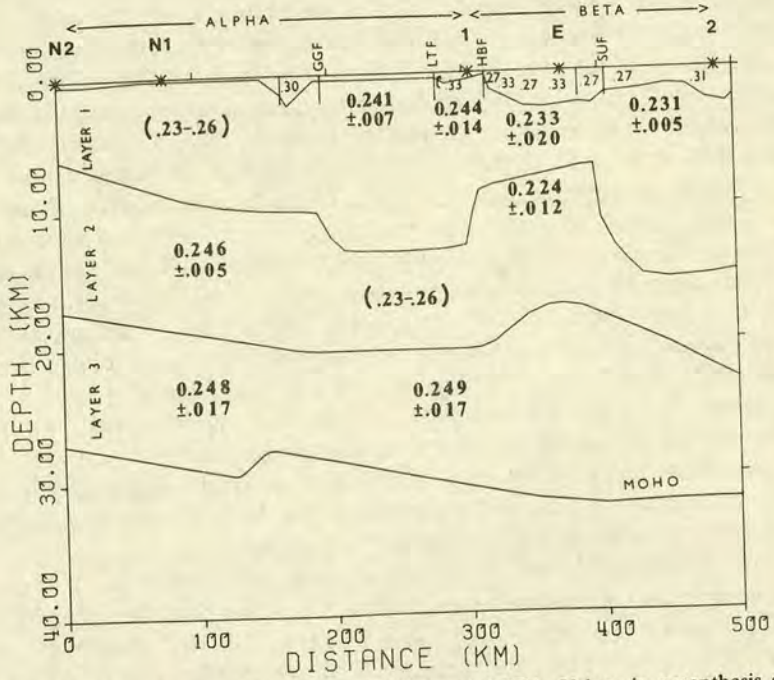

Figure 7. Poisson's ratio structure of segments ALPHA and BETA. Values in parenthesis are assumed range of σ. Uncertainties correspond to ± two standard deviations.

6 Results

Results of the Poisson's ratio modelling for segment BETA and ALPHA are shown in Fig. 7: the fits are reasonably good and some theoretical curves from the model are shown in Figs 4 and 5.

6.1 SEGMENT BETA

Shear wave sedimentary phases (distances less than about 10 km) did not have onsets sharp enough to define the average Poisson's ratio for the sediments with good resolution. Nevertheless these near-shot arrivals indicate that the average σ for the sedimentary layers lies roughly in the range 0.25 to 0.34. On the other hand in order to get a good fit to the t_s/t_p data for phase a_0, the sediments under shot points 1, E and 2 must have σ greater than 0.30. The various values of σ in the Midland Valley sedimentary layers between shots 1 and E (Fig. 7) were so chosen to account for relative high and low values of t_s/t_p on profiles 1 – BETA and E – BETA + ALPHA. For example $\sigma = 0.33$ to the south of the Highland Boundary Fault, Fig. 7, accounts for the relative high t_s/t_p of shot 1 – BETA at 22 km distance (Fig. 5(a)) and one from E – BETA + ALPHA at 46 km distance (Fig. 5(c)). The values of σ shown in the model of Fig. 7 for the sedimentary and superficial layers have then uncertainties around ± 0.03 and should be regarded as mere sedimentary corrections, or a kind of weathering correction in terms of Poisson's ratio. The important point is that this uncertainty of ± 0.03 does not significantly affect the determination of σ for the lower refractors a_0 and a_1. For example if under shot E, as shown in Fig. 7, σ was decreased by 0.03, σ for the a_0 refractor (layer 1) should be increased by only 0.007 to give the same t_s/t_p ratio at a distance of 40 km.

Although the overall fit for segment BETA is good, there is one misfit: phase a_0, 1 – BETA, near 40 km (Fig. 5(a) – theoretical curve too high) and phase a_1, E – BETA + ALPHA around 50 km (Fig. 5(c) – theoretical curve too low). It is difficult to improve the fit for shot 1 without worsening the fit for shot E. This suggests that a constant Poisson's ratio for layer 1 under the Midland Valley is not a very good approximation. Lower values of σ in the northern part and higher in the southern part (under shot point E) would probably correct that misfit. Nevertheless the data are not enough to justify the inclusion of one more parameter in the model and an average value of $\sigma = 0.233 \pm 0.020$ under the Midland Valley is retained.

No information is available for the bottom of the crust as deep reflections from this part of the profile were almost absent. This may be due in part, to the development of a relatively complex deep structure (Bamford *et al.* 1978).

6.2 SEGMENT ALPHA

For the northern part of ALPHA, no information about layer 1 is available as the *S* arrivals of shot N1 and N2 for phases a_0 and a_1 are too emergent. An assumed range of possible values from 0.23 to 0.26 was used for layer 1 in order to calculate σ for deeper layers.

In the southern part of ALPHA layer 1 has σ well determined by phase a_0 from shot 1 (at least in the upper part of layer 1, as explained before), but no information is available for layer 2. The same range of 0.23 to 0.26 for layer 2 was used to calculate σ for layer 3.

Poisson's ratio for layer 2 in the northern part of ALPHA is fairly well determined with phase e from shot N2 (reflection from the bottom of layer 2), Figs 2(b) and 4. In spite of the uncertainties in σ for the layer above it, σ for layer 2 was determined as 0.246 ± 0.005. This should be understood as an average of Poisson's ratio along layer 2 (say from a horizontal distance of 40 to 170 km). There is however, general agreement between this value and

one calculated from the ratio of apparent velocities determined by Smith & Bott (1975) for the same layer further north of the LISPB line, on a profile between Cape Wrath and Shetland. Their P and S velocities of 6.40 ± 0.09 and 3.76 ± 0.05 km/s respectively give $\sigma = 0.236 \pm 0.015$.

Poisson's ratios for the bottom of the crust have relatively larger uncertainties due to: (a) greater uncertainties in shear c onsets (compressional c can be picked to about ± 0.05 s after correlation processes are applied) and (b) uncertainties in σ of the upper layers, although in a smaller proportion, being transmitted to deeper layers.

7 Conclusion

The analysis of LISPB data demonstrates that explosions can be used in the study of shear waves and determination of crustal Poisson's ratios when three-component stations are employed. Although the signal to noise ratios of S waves from explosions are not usually as large as those from earthquakes, this deficiency is more than compensated for by the known origin time and high station density along a profile.

Difficulties in picking shear-wave arrivals are not only due to the fact that they are secondary arrivals (and so will always appear in a background of signal generated noise following the P waves), but also seem to be related to a more complicated type of ground motion (as compared to P waves) for shallow angle arrivals, depending strongly on the station site. Because of these difficulties S apparent velocities determined directly from the seismic sections have relatively large uncertainties. In contrast, use of the S to P travel-time ratio can sometimes allow the determination of Poisson's ratio with accuracies better than 0.01, as in layer 1 under the Southern Uplands and in layer 2 north of the Great Glen Fault.

LISPB Poisson's ratios were generally close to the conventional 0.25, except for layer 1 in the Southern Uplands ($\sigma = 0.231$) and layer 2 under the Midland Valley ($\sigma = 0.224$). These low values may indicate that these layers have anomalous physical properties possibly as a result of tectonic activity close to the Southern Uplands Fault. This would appear to confirm the region of the Southern Uplands Fault as a major point of interest in studies of Caledonian tectonics (Bamford *et al.* 1978).

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References

Bamford, D., Faber, S., Jacob, B., Kaminski, W., Nunn, K., Prodehl, C., Fuchs, K., King, R. & Willmore, P., 1976. A lithosphere seismic profile in Britain – I. Preliminary results, *Geophys. J. R. astr. Soc.*, **44**, 145–160.

Bamford, D., Nunn, K., Prodehl, C. & Jacob, B., 1978. LISPB – IV. Crustal structure of Northern Britain, *Geophys. J. R. astr. Soc.*, **54**, 43–60.

Birch, F., 1969. Density and composition of the Upper Mantle: first approximation as an Olivine layer, in *The Earth's crust and upper mantle*, AGU monograph **13**, 18.

Christensen, N. I., 1965. Compressional wave velocities in metamorphic rocks at pressures to 10 kb, *J. geophys. Res.*, **70**, 6147–6164.

Christensen, N. I., 1966. Shear wave velocities in metamorphic rocks at pressures to 10 kb, *J. geophys. Res.*, **71**, 3549–3556.

Erickson, E. L., Miller, D. E. & Waters, K. H., 1968. Shear wave recordings using continuous signal methods, part II – later experiments, *Geophys.*, **33**, 240–254.

Geyer, R. L. & Martner, S. T., 1969. *SH* waves from explosive sources, *Geophys.*, **34**, 893–905.

Gregory, A. R., 1976. Fluid saturation effects on dynamic elastic properties of sedimentary rocks, *Geophys.*, **41**, 895–921.

Jolly, R. N., 1956. Investigation of shear waves, *Geophys.*, **21**, 905–938.

King, M. S., 1966. Wave velocity in rocks as a function of changes in overburden pressure and pore fluid saturants, *Geophys.*, **31**, 50–73.

Meissner, R., 1965. *P* and *SV*-waves from uphole shooting, *Geophys. Prosp.*, **13**, 433–459.

Montalbetti, J. F. & Kanasewich, E. R., 1970. Enhancement of teleseismic body phases with a polarization filter, *Geophys. J. R. astr. Soc.*, **21**, 119–129.

Nuttli, O., 1961. The effect of the Earth's surface on the *S* wave particle motion, *Bull. seism. Soc. Am.*, **51**, 237–246.

Scarascia, S., Colombi, B. & Cassinis, R., 1976. Some experiments on transverse waves, *Geophys. Prosp.*, **24**, 549–568.

Simmons, G., 1964. Velocity of shear waves in rocks to 10 kb, 1, *J. geophys. Res.*, **69**, 1123–1130.

Smith, P. J. & Bott, M. H. P., 1975. Structure of the crust beneath the Caledonian Foreland and Caledonian Belt of the North Scottish shelf region, *Geophys. J. R. astr. Soc.*, **40**, 187–205.

Tatham, R. H. & Stoffa, P. L., 1976. V_p/V_s – a potential hydrocarbon indicator, *Geophys.*, **41**, 837–849.